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Postrelease Survival, Vertical And Horizontal Movements, And Thermal Habitats Of Five Species Of Pelagic Sharks In The Central Pacific Ocean

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Abstract—From 2001 to 2006, 71 pop-up satellite archival tags (PSATs) were deployed on five species of pelagic shark (blue shark [*Prionace glauca*]; shortfin mako [*Isurus oxyrinchus*]; silky shark [*Carcharhinus falciformis*]; oceanic whitetip shark [*C. longimanus*]; and bigeye thresher [*Alopias superciliosus*]) in the central Pacific Ocean to determine species-specific movement patterns and survival rates after release from longline fishing gear. Only a single postrelease mortality could be unequivocally documented: a male blue shark which succumbed seven days after release. Meta-analysis of published reports and the current study ($n=78$ reporting PSATs) indicated that the summary effect of postrelease mortality for blue sharks was 15% (95% CI, 8.5–25.1%) and suggested that catch-and-release in longline fisheries can be a viable management tool to protect parental biomass in shark populations. Pelagic sharks displayed species-specific depth and temperature ranges, although with significant individual temporal and spatial variability in vertical movement patterns, which were also punctuated by stochastic events (e.g., El Niño-Southern Oscillation). Pelagic species can be separated into three broad groups based on daytime temperature preferences by using the unweighted pair-group method with arithmetic averaging clustering on a Kolmogorov-Smirnov D_{\max} distance matrix: 1) epipelagic species (silky and oceanic whitetip sharks), which spent >95% of their time at temperatures within 2°C of sea surface temperature; 2) mesopelagic-I species (blue sharks and shortfin makos, which spent 95% of their time at temperatures from 9.7° to 26.9°C and from 9.4° to 25.0°C, respectively; and 3) mesopelagic-II species (bigeye threshers), which spent 95% of their time at temperatures from 6.7° to 21.2°C. Distinct thermal niche partitioning based on body size and latitude was also evident within epipelagic species.

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Postrelease survival, vertical and horizontal movements, and thermal habitats of five species of pelagic sharks in the central Pacific Ocean

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Although there is considerable disagreement and uncertainty about the current state of pelagic fish populations (Burgess et al., 2005; Hampton et al., 2005; Sibert et al., 2006), there is general agreement that large apex predators, particularly sharks, are at greatest risk of overfishing (Baum et al., 2003; Baum and Myers, 2004; Camhi, 2008). Possessing life-history characteristics (e.g., slow growth, long gestation, late maturity) that evolved in the absence of industrial fishing, pelagic shark species are susceptible to overfishing, and declining trends in some populations need to be reversed for parental biomass to rebuild stocks (Camhi, 2008; Chang and Liu, 2009; Dulvey et al., 2008). With food web models, Schindler et al. (2002) predicted that continued mortality of blue shark (*Prionace glauca*) in longline fisheries in the central Pacific could adversely affect their populations and the role of this species as apex

predators. Moreover, commercial and recreational fishing activities generally remove the largest animals (i.e., parental biomass) and heavy selection pressure over several decades can potentially cause evolutionary effects (e.g., heritable changes in life-history traits such as body size, growth, age-at-maturity, and fecundity; Law, 2000; DiBattista et al., 2009; Genner et al., 2009).

Large pelagic sharks, particularly blue sharks, which form a large part of the international shark fin trade (Clarke et al., 2006), are generally not targeted but are by far the majority of the bycatch in pelagic gill nets and longline fisheries targeting swordfish (*Xiphias gladius*) (Camhi, 2008; Mandelman et al., 2008; Nakano and Stevens, 2008). Effective strategies to mitigate shark bycatch requires knowledge of species-specific horizontal and, more importantly, vertical movement patterns (e.g., Wat-

son et al., 2009). Knowledge of these vertical movement patterns may allow fishing crews to target the opportunity of mismatch between hook depth and the sharks' vertical distributions and thus possibly minimize bycatch (Beverly et al., 2009). For effective management measures to be implemented, it is also beneficial to have accurate estimates of both at-vessel and postrelease mortality rates (Carruthers et al., 2009). These data are necessary for estimating total fishery-induced mortality and for improving stock assessments (Kitchell et al., 2004). Mitigation strategies could then be given special consideration for species with high rates of postrelease mortality (Carruthers et al., 2009).

Information on postrelease mortality in blue sharks (Carey and Scharold, 1990; Weng et al., 2005; Moyes et al., 2006; Campana et al., 2009a; Queiroz et al., 2010; Stevens et al., 2010), bigeye threshers (*Alopias superciliosus*) (Nakano et al., 2003; Weng and Block, 2004), shortfin makos (*Isurus oxyrinchus*) (Holts and Bedford, 1993; Klimley et al., 2002; Sepulveda et al., 2004; Loefer et al., 2005), and common thresher sharks (*A. vulpinus*) (Heberer et al., 2010) is available from studies with acoustic tracking and pop-up satellite archival tags (PSATs). In two studies (Moyes et al., 2006; Campana et al., 2009a), the investigation of postrelease mortality of blue sharks released from longline fishing gear was the primary goal, but mortality rates may have been confounded by specific aspects of fishing practices (Musyl et al., 2009). Hook type, time spent hooked on the line, fight time, leader material, fish size, and handling and discard practices can influence the at-vessel and postrelease mortality of pelagic shark species (e.g., Diaz and Serafy, 2005; Moyes et al., 2006; Campana et al. 2009a; Carruthers et al., 2009; Heberer et al. 2010; Hoey and Moore¹).

Our goals were to measure postrelease mortality rates and vertical movement patterns in the five most commonly captured pelagic shark species in the Hawaii-based commercial longline fishery: blue sharks, bigeye threshers, oceanic whitetip sharks (*Carcharhinus longimanus*), shortfin makos, and silky sharks (*C. falciiformis*) (Walsh et al., 2009). All five species represent a significant portion of the shark bycatch in global fisheries and their life history characteristics make populations vulnerable to fishing pressure (Cortés, 2000; Camhi, 2008; Dulvy et al., 2008; Stevens, 2008; Chang and Liu, 2009). Moreover, there is little or no information about their postrelease survival, population ecology, and movement patterns in the central Pacific Ocean. As far as we know, there are no published reports on the movements and postrelease mortality of silky sharks and oceanic whitetip sharks, and several authors have commented on the paucity of information on the biology

and ecology of these apex predators (Bonfil, 2008; Bonfil, et al., 2008; Dulvy et al., 2008). Results from this study extend the work presented in Moyes et al. (2006) and are expected to be useful in the mitigation of shark bycatch and mortality.

Materials and methods

Sharks were caught by pelagic longline fishing gear (from March 2001 through November 2006) deployed from the NOAA research vessels *Townsend Cromwell* and *Oscar Elton Sette* and by using methods described in Moyes et al. (2006). In brief, longline gear (~400–800 hooks per set) was deployed at night (usually immediately after dusk) and retrieved in the morning. Because we used four to six hooks between floats; hook depths were generally <100 m as determined by attached time-temperature-depth recorders (Wildlife Computers, Redmond, WA).

Soak times ranged from 10 to 24 hours with an average of 15 hours, and before 2004, we employed 15/0 size circle hooks, squid (*Illex* spp.) bait, and green chemical light sticks attached to the monofilament nylon leader ~90 cm above each hook. However, because of regulations introduced in 2004 to reduce sea turtle bycatch in the Hawaii-based shallow-set (nighttime) commercial longline fishery targeting swordfish (Gilman et al., 2007; Walsh et al., 2009), we began using 16/0 and 18/0 circle hooks (no offset), and Pacific saury (sanma, *Cololabis saira*) as bait. In addition, to improve shark catch rates by reducing bite-offs from monofilament leaders, we added ~25 cm of seven-strand braided stainless steel cable immediately above the hook.

Sharks were hoisted aboard by a sling and restrained by the crew as described in Moyes et al. (2006). Sharks showing an absence of movements or reaction of the nictitating membrane to light touching of the eye were deemed dead and were not tagged (i.e., these samples would bias the postrelease mortality estimate). Tagged sharks were measured to the nearest centimeter for total length (TL), and hooks were removed by cutting them in half with bolt cutters unless they were too deeply ingested, in which case, the leader line was cut as close to the mouth of a shark as possible. PSATs (model PTT-100, Microwave Telemetry, Columbia, MD) were affixed to the dorsal fin by drilling a 10–15 mm diameter hole near the base of the fin and threading seven-strand braided stainless steel cable encased in soft plastic tubing (which acted as the harness) through the wound. Next, a second tether (made of ~123-kg breaking strength fluorocarbon leader material) was used to attach (with stainless steel crimps and thimbles) the PSAT to the dorsal fin harness. The only exception was applied to bigeye threshers, which were tagged in the water by using a harpoon, and for these sharks the tag head was affixed to the end of the tethers on the PSAT. For these sharks, total lengths were visually estimated.

PSATs were programmed to acquire temperature and pressure (depth) readings every 15–60 minutes and

¹ Hoey, J. J., and N. Moore. 1999. Captain's report: multi-species catch characteristics for the U.S. Atlantic pelagic longline fishery. National Fisheries Inst. report to NOAA, National Marine Fisheries Service, Silver Spring, MD, 78 p. [Available from <http://www.sefsc.noaa.gov/seaturtlecontractreports.jsp>, accessed May 2011.]

pop-up dates were set at 8–13 months after deployment of the tags. Depth and temperature data were measured as 8-bit numbers, yielding a depth resolution of ~5.4 m and temperature resolution of ~0.17°C. Fail-safe options were also programmed into the PSAT software whereby stationary PSATs (i.e., those experiencing no significant changes in pressure) or shed tags would begin transmitting archived data to the ARGOS satellite system after four days. In the event of mortality, once the shark sank to ~1200 m and remained there for ~15 minutes, the PSAT would separate from the shark, float to the surface, and begin transmitting stored data to ARGOS.

Daily (raw) geolocation estimates were calculated by the manufacturer using ambient light-level irradiance data during postprocessing of the satellite data with a proprietary algorithm (Gunn and Block, 2001). From the raw geolocations, most probable tracks (MPTs), movement parameters, and associated error estimates were calculated by a state-space Kalman filter algorithm with position estimates refined with the use of sea surface temperature (SST) (Nielsen et al., 2006). Depth and temperature data were assigned to daytime or nighttime according to times of local dusk and dawn derived from longitude and latitude estimates (from the MPTs) with the use of standard astronomical formulae (Meeus, 1998).

Resampling techniques were used to construct 95% parametric bootstrap confidence intervals (CI*) (with the assumption of a binomial distribution with 10,000 replicates) for postrelease mortality estimates and PSAT reporting rates (Manly, 2007). Meta-analysis was used to estimate a summary effect for postrelease mortality in blue sharks from published studies (Weng et al., 2005; Campana et al., 2009a; Stevens et al., 2010) and the present report, by assuming that these studies represent random samples of some population in which the underlying (infinite-sample) effect sizes have a distribution rather than a single value (i.e., random effects model, Borenstein et al., 2009). The analysis was conducted on the logit (log odds ratio) of the proportion of blue sharks that ultimately died as identified from PSATs across studies by using Comprehensive Meta Analysis, vers. 2.2 (www.Meta-Analysis.com, accessed November 2010). Postrelease mortality estimates and 95% confidence intervals were weighted by sample size and the number of studies where heterogeneity was assumed (i.e., with the random-effects model where each study was assumed to have its own postrelease mortality rate and variance). The Q statistic, a measure of heterogeneity, was calculated to test whether postrelease mortality estimates across studies were similar, and the Z test was used to determine whether the postrelease mortality estimate was significantly greater than zero (Borenstein et al., 2009). If postrelease mortality is consistent across studies, then the meta-analysis yields a combined estimate that is more precise than any of the separate estimates (Borenstein et al., 2009). For presentation purposes, logits were converted back into percentages.

Data provided by the PSATs were divided into six data streams by parsing depth data into day depth (DD), night depth (ND), and “all” depth (=both day and night) (AD); and temperature data into day temperature (DT), night temperature (NT), and combined temperature (AT). Nonparametric tests were used to examine variation by species with Kruskal-Wallis ANOVAs (to compare equality of medians across individuals) for each of the data streams where the test statistic (H_c) was adjusted for ties (Zar, 1996) because data distributions were not normally distributed (Lillifors tests, $P < 0.01$). For each species, multiple *post-hoc* pairwise Mann-Whitney W-tests, with Bonferroni corrected P -values to account for inflation of type-I error based on multiple tests of the same hypothesis (MWBC), were used to compare equality of medians within and between individuals for each of the data streams (Zar, 1996). When only a single Mann-Whitney test could be performed, Monte Carlo methods (10,000 random assignments) were used to obtain an empirical P -value that approximated the exact P -value without reliance on asymptotic distributional theory or exhaustive enumeration (Manly, 2007). The greatest vertical distance (D_{\max}) between cumulative distribution functions among tags from two-sample Kolmogorov-Smirnov (KS) tests was formatted into distance matrices as input for the unweighted pair-group method by using arithmetic average (UPGMA) clustering (Sneath and Sokal, 1973; Musyl et al., 2003). This procedure allowed us to observe patterns of depth and temperature preferences across pelagic species. Electronic tag data from Pacific bigeye tuna (*Thunnus obesus*) (Musyl et al., 2003), swordfish, black marlin (*Istiompax indica*), and blue marlin (*Makaira nigricans*) (Musyl et al.²) served as outgroups to help clarify and define relationships (Sneath and Sokal, 1973). The cophenetic correlation was used as a measure of goodness-of-fit between the matrices and resultant clustering dendrograms (e.g., 0.7–0.8 is considered “poor,” >0.8 is considered “good,” and >0.9 is considered “very good” [Rohlf, 1992]).

Time-at-depth and time-at-temperature data were aggregated into 20-m and 1°C bins, respectively. These data were subsequently expressed as a fraction of the total time of observation for each shark, and the fractional data bins were averaged across all sharks within each category. For sharks experiencing several lunar cycles, the correlation coefficient (R) was determined between average nighttime depth (m) and lunar illumination (Zar, 1996). Lunar illumination data were obtained from the United States Naval Observatory (<http://aa.usno.navy.mil/data/docs/MoonFraction.php>, accessed June 2010) and were uncorrected for cloud

² Musyl, M. K., L. M. McNaughton, J. Y. Swimmer, and R. W. Brill. 2004. Convergent evolution of vertical movement behavior in swordfish, bigeye tuna and bigeye threshers. Vertical niche partitioning in the pelagic environment as shown by electronic tagging studies. Pelagic Fisheries Research Program, Univ. Hawaii Manoa, Newsletter 9:1–4.

cover. Unless indicated otherwise, all statistical tests were performed at the $P=0.05$ level of significance.

Results

Rates of at-vessel and postrelease mortality

Capture date, sizes, deployment location, set pop-off date, ARGOS reporting location, days-at-liberty, and linear displacement for tagged sharks are summarized in Table 1. The overall PSAT reporting rate was 62% ($CI^*=50\text{--}73\%$), although reporting rates varied by species: 100% for silky sharks; 81% ($CI^*=63\text{--}98\%$) for oceanic whitetip sharks; 50% ($CI^*=34\text{--}65\%$) for blue sharks; 40% ($CI^*=0\text{--}80\%$) for shortfin makos; and 38% ($CI^*=13\text{--}75\%$) for bigeye threshers. Median days-at-liberty were likewise species-specific: bigeye threshers, 240 days (range: 181–240 days); shortfin makos, 165 days (155–174 days); oceanic whitetip sharks, 164 days (10–243 days); blue sharks, 86 days (1–247 days); and silky sharks, 73 days (12–194 days).

The fraction of sharks found dead during gear retrieval was species-specific and was concordant with estimates derived from the commercial fishery (Table 2). More importantly, we were able to document only one case of postrelease mortality out of the 44 sharks (2.3%, $CI^*=0\text{--}6.8\%$) whose PSAT transmitted data. One blue shark (male, 173 cm TL) expired seven days after being released (one mortality in 16 reporting tags affixed to blue shark; 6.3%, $CI^*=0\text{--}19\%$).

Meta-analysis indicated the summary effect (Table 3) for postrelease mortality in blue sharks was 15% (95% CI, 8.5–25.1%). The Z statistic indicated that postrelease mortality was significantly different from zero ($P<0.001$) and the Q statistic indicated studies were measuring the same parameter ($P=0.680$). Although the narrower 95% CI bounds for the summary effect (Table 3) indicated increased power over individual studies; a comparison of postrelease mortality estimates between Campana et al. (2009a) and the present study for blue sharks (with the assumption that sharks have equal chance of survival) at 80% power would require ~275 reporting PSATs (two-tailed Z-tests between two independent proportions at $\alpha=0.05$, Zar, 1996).

Horizontal movements

For each of the pelagic shark species, estimated most probable tracks are shown in Figure 1. Error estimates for longitude were much lower than those for latitude in the movement model (Appendix 1). Geolocations could not be calculated for PSATs attached to bigeye threshers (Fig. 1F) because of extreme and rapid vertical excursions coinciding at crepuscular times and the inability of the light sensor to record these changes (Musyl et al., 2001, 2003).

For species where geolocation data were available, some individuals exhibited more directed movements as indicated by their advection-diffusion parameters

whereas other movement patterns were more complex or cyclical (Fig. 1, Appendix 1). For example, the advection parameters for longitude ($u=9.23$) and latitude ($v=3.84$) indicated primarily east–west movements by the shortfin mako with ID 38572 (female, 210 cm TL) when it swam from subtropical waters near Hawaii to temperate waters in the North Pacific, including California Current coastal waters off central California (Fig. 1E). Tagged silky sharks traveled west and southwest of the Hawaiian Islands in 20–2004, but south of 10°N in 2005, near the North Equatorial Countercurrent (NEC) (Fig. 1C). The diffusion parameters estimated from the movement model indicated that six sharks exhibited relatively meandering swimming behaviors whereas three individuals (IDs 46585, 38581, 38573) exhibited more north–south directed movements. Oceanic whitetip sharks showed a complex movement pattern generally restricted to central Pacific tropical waters north of the NEC (Fig. 1D). Nine individuals exhibited meandering swimming behavior, whereas three sharks (IDs 13113, 38582, 46568) generally adopted more straight-line swimming modes, of which one shark (ID 38582) made a directed southward movement across the equator into the South Pacific. Although restricted to central Pacific tropical waters north of the NEC, blue sharks showed complex movement patterns (Fig. 1, A and B) from waters near Hawaii into the Subtropical Convergence Zone. As determined from deployment and pop-up locations, blue sharks tagged in 2001 occupied latitudes from 7.92° to 30.75°N (Fig. 1A), but individuals tagged in 2002 did not travel farther south than 17.6°N (Fig. 1B).

Vertical movements

Blue sharks remained significantly deeper and experienced significantly cooler temperatures during the day than during the night (Fig. 2; Appendices 2 and 3). Moreover, the significant daytime and nighttime differences in depth and temperature preferences were evident within and across individuals, and also when the data were grouped by sex (Figs. 2 and 3; Appendices 2 and 3). As identified by the coefficient of variability, daytime and nighttime vertical movement patterns were similar, but the vertical movements of male blue sharks were significantly more variable than those of females. Coefficients of variability over 1.0 have been used to indicate possible mixtures in samples (Simpson et al., 1960) and values over 1.0 in blue sharks are reflective of individuals switching from a typical deep-daytime to shallow-nighttime vertical movement pattern, or exhibiting a mixture of the two patterns (Fig. 2). The aggregated temperature-depth profile (Fig. 2B) shows that blue sharks regularly undertake movements beneath the uniformed temperature surface layer, but with considerable variability at crepuscular transitions (Fig. 2E). Several blue sharks adjusted their nighttime behaviors simultaneously with changing lunar illumination (Appendix 2).

Bigeye threshers showed the most striking differences in depth and temperature preferences and all MWBC

Table 1

Tagging details for pop-up satellite archival tags (PSATs) affixed to blue shark (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*), silky shark (*Carcharhinus falciformis*), oceanic whitetip shark (*C. longimanus*) and bigeye thresher (*Alopias superciliosus*). Total length (TL) was measured to the nearest cm. Set pop-off date is the programmed time PSATs were scheduled to report data after deployment. The locations where the PSATs were deployed and reported from in latitude and longitude east are given in decimal degree format. DAL=days-at-liberty, nr=nonreporting tag, M=male, F=female, and linear displacement of PSATs from deployment to reporting locations in nautical miles (nmi).

PSAT no. and sex	TL (cm)	Tagging date	Set pop-off date	Deployment latitude	Deployment longitude	Reporting date	Reporting latitude	Reporting longitude	DAL	Linear displac. (nmi)
Blue shark										
<i>(Prionace glauca)¹</i>										
13081F	168	03/30/01	06/29/01	29.06	199.09	03/31/01	21.76	201.10	4	451.31
13083F ^a		04/05/01	10/03/01	18.79	201.61	05/10/01	23.36	197.99	35	340.92
13085F	168	04/02/01	09/30/01	18.77	201.68				nr	
13087M	204	04/05/01	05/05/02	18.81	201.64	04/27/01	25.82	194.77	22	567.47
13088M	152	04/10/01	05/10/02	18.88	201.72				nr	
13089F ^a	160	04/10/01	05/10/02	29.07	199.05				nr	
13091M ^b	173	04/11/01	05/11/02	28.29	201.28	04/16/01	18.91	201.10	5	562.89
13093F	160	04/11/01	05/11/02	28.30	201.33	07/22/01	29.40	216.34	102	791.03
13094F ^a		04/05/01	05/05/02	28.28	201.24				nr	
13095F	160	04/03/01	05/03/02	29.08	199.02	05/23/01	17.21	192.93	50	787.07
13096F	173	04/03/01	05/03/02	30.31	201.50	06/11/01	7.92	200.05	69	1345.87
13097F	183	04/02/01	05/02/02	30.75	200.01	08/23/01	26.45	199.50	143	259.39
13098F ^a	150	04/05/01	05/05/02	30.31	201.50	11/24/01	22.38	188.62	233	839.20
13111F ^{c-1}	152	04/14/01	05/14/02	30.26	201.93	06/10/01	13.91	199.54	41	989.87
13209M	140	04/09/02	12/10/02	28.48	202.09				nr	
13215F	200	04/07/02	12/08/02	31.02	199.97	12/10/02	28.56	191.30	247	474.81
13218F ^a	145	04/06/02	12/07/02	31.02	199.97				nr	
13225M	131	04/05/02	12/06/02	31.01	199.96				nr	
13226M	133	04/10/02	12/11/02	31.01	199.97				nr	
13475M	120	04/10/02	12/11/02	31.03	199.99				nr	
13478M ^d		04/10/02	12/11/02	30.24	201.93				nr	
13491F	215	04/10/02	12/11/02	31.01	199.96	12/10/02	24.06	189.58	244	691.39
13497F ^a	200	04/10/02	12/11/02	21.56	201.43	05/16/02	35.18	206.29	36	856.19
13499F ^{e2}	175	04/06/02	12/07/02	31.01	199.96	12/08/02	17.60	183.69	246	1196.73
13501M	196	04/10/02	12/11/02	30.70	199.93				nr	
13503F	187	04/02/02	12/03/02	31.10	199.90	07/31/02	25.08	209.39	120	618.26
27322M	148	04/10/02	12/11/02	30.96	199.92	12/10/02	34.07	206.03	244	360.98
27323M	180	04/09/02	12/10/02	31.13	199.94				nr	
29149F	200	04/12/02	12/13/02	30.99	199.95				nr	
29537M	160	04/10/02	12/11/02	26.64	201.97				nr	
29541M	158	04/12/02	12/13/02	30.93	198.59				nr	
29872M	180	04/10/02	12/11/02	19.10	201.83				nr	

continued

Table 1 (continued)

PSAT no. and sex	TL (cm)	Tagging date	Set pop- off date	Deployment latitude	Deployment longitude	Reporting date	Reporting latitude	Reporting longitude	DAL	Linear displac. (nmi)
Shortfin mako (<i>Isurus oxyrinchus</i>) ²										
13496M	185	04/04/02	12/05/02	26.64	201.97				nr	
28721M	118	04/13/02	12/14/02	30.93	198.59				nr	
30371M	190	04/24/02	12/25/02	19.10	201.83				nr	
38572F	210	12/03/02	08/06/03	21.78	203.70	05/07/03	28.94	231.81	155	1579.10
46583F		11/15/06	07/17/07	18.83	201.68	05/08/07	18.55	199.45	174	127.85
Silky shark (<i>Carcharhinus falciformis</i>) ³										
38573M	170	12/09/02	08/12/03	19.01	203.90	04/20/03	9.67	197.05	132	687.15
38581F	140	12/12/02	08/15/03	19.34	202.92	01/12/03	13.80	195.27	31	551.20
38599M	200	04/02/03	12/02/03	19.25	203.71	05/08/03	18.85	200.25	36	197.69
38601M	200	12/11/02	08/14/03	19.47	203.95	06/23/03	21.42	200.22	194	240.12
46564M		02/11/05	10/13/05	7.34	197.06	03/03/05	6.63	198.09	20	74.68
46566M		02/07/05	10/09/05	6.86	197.22	03/04/05	6.88	205.56	25	496.80
46571M	168	05/20/04	01/19/05	19.37	202.83	06/01/04	19.90	201.48	12	82.65
46585M	120	02/05/05	10/07/05	5.24	198.50	05/26/05	6.01	191.44	110	424.08
46588M	137	05/09/04	01/08/05	18.13	201.59	10/01/04	18.41	199.66	145	111.24
46590F	116	02/01/05	10/03/05	8.13	199.73	03/01/05	7.71	206.31	28	391.84
Oceanic whitetip shark (<i>Carcharhinus longimanus</i>) ⁴										
13092F	120	04/13/01	05/13/02	19.46	203.90	09/24/01	23.84	186.61	164	998.57
13113M		02/07/05	10/09/05	8.10	199.64	08/01/05	7.82	182.46	175	1020.93
29487F	107	04/25/02	12/26/02	19.27	203.97				nr	
29918F	225	04/21/02	12/22/02	19.21	203.85	05/01/02	18.88	198.20	10	321.04
38574M	100	12/07/02	08/09/03	18.36	201.71				nr	
38575M	200	12/04/02	08/07/03	21.36	204.14	07/07/03	25.40	201.73	215	276.34
38576M	200	12/05/02	08/07/03	19.42	203.92	05/03/03	19.02	207.41	149	199.18
38582M	115	12/07/02	08/10/03	29.08	199.01	03/12/03	-9.30	195.01	95	2314.41
38598M	200	04/03/03	06/03/03	19.58	203.73	06/03/03	16.48	198.06	61	373.10
46568M		05/16/04	01/15/05	18.55	204.52	08/10/04	23.77	193.07	86	712.72
46569M	127	02/01/05	10/03/05	19.49	203.98	06/18/05	8.73	191.71	137	961.60
46570F		05/14/04	01/13/05	18.25	201.51	01/02/05	15.28	202.12	233	181.61
46579M	120	02/06/05	10/08/05	5.97	197.57				nr	
46581M	100	05/22/04	01/21/05	19.60	203.71	12/14/04	16.26	200.23	206	282.15
46587M		05/09/04	01/08/05	18.13	201.55	01/07/05	16.18	201.58	243	117.01
46589F		05/20/04	01/19/05	19.37	202.88	01/17/05	19.21	201.53	242	77.05

continued

Table 1 (continued)

PSAT no. and sex	TL (cm)	Tagging date	Set pop-off date	Deployment latitude	Deployment longitude	Reporting date	Reporting latitude	Reporting longitude	DAL	Linear displac. (nmi)
Bigeye thresher (<i>Alopias superciliosus</i>)⁵										
28476 ^e		04/28/02	12/29/02	18.52	201.97	12/24/02	16.45	234.67	240	1872.98
29290 ^e		04/27/02	12/28/02	18.55	202.17				nr	
29481 ^e	200	04/27/02	12/28/02	18.57	202.08	12/23/02	19.84	198.66	240	208.22
29896 ^e		04/27/02	12/28/02	18.56	202.11				nr	
30028 ^e		04/28/02	12/29/02	18.52	201.96				nr	
30373 ^e		04/27/02	12/28/02	18.55	202.13				nr	
38597 ^f	200	04/01/03	05/31/03	18.71	203.19				nr	
46582 ^f		05/21/04	01/20/05	19.39	202.84	11/18/04	19.72	229.97	181	1532.40

¹⁻⁵ Estimated lengths at maturity (given in cm of total length [TL]), M=male, F=female.

¹ Blue shark: ~200 cm for both sexes (M: 182–235 cm, F: 173–229 cm, Nakano and Stevens, 2008).

² Shortfin mako, M: 195–202 cm, F: 265–312 cm (Stevens, 2008).

³ Silky shark, M: 180–210 cm, F: 180–218 cm (Bonfil, 2008).

⁴ Oceanic whitetip, M: 168–196 cm, F: 175–189 cm (Bonfil et al., 2008).

⁵ Bigeye thresher, M: 270–288 cm, F: 332–341 cm (Smith et al., 2008).

^a Nuptial bites present on dorsal, pectoral fins and body.

^b Postrelease mortality (see also Moyes et al., 2006).

^{c1} Hook ingested and stomach everted at capture; specimen recaptured by Japanese longline fishing vessel on 25 May, 2001; 41 days at-liberty, conventional plastic tag no.1649 recovered in addition to PSAT and harness (no cuts, abrasions on PSAT or harness)

^{c2} Hook ingested, stomach everted.

^d PSAT likely damaged during release.

^e PSATs affixed with metal tag heads near base of dorsal fin by using a harpoon (Musyl et al. 2011).

^f PSATs affixed with flopper tag heads (i.e., nylon tag head augmented with stainless steel spear gun blades, Musyl et al., 2011) near base of dorsal fin by using a harpoon.

Table 2

Number of pelagic sharks caught and those retrieved dead from shallow-set longline gear targeting swordfish (*Xiphias gladius*). Mortality estimates from the Hawaii-based commercial longline fishery are provided for comparison (na=not available).

Species	No. caught	Samples ¹ taken	No. dead	% dead	% dead commercial fishery ²	
					Shallow	Deep
Blue shark (<i>Prionace glauca</i>)	203	37	12	5.9	5.7	4.0
Crocodile shark (<i>Pseudocarcharias kamoharai</i>)	3	2	2	66.7	na	13.6
Oceanic whitetip shark (<i>Carcharhinus longimanus</i>)	19	6	1	5.3	7.4	20.7
Shortfin mako (<i>Isurus oxyrinchus</i>)	8	4	0	0	20.5	7.5
Silky shark (<i>Carcharhinus falciformis</i>)	35	3	4	11.4	na	21.8
Bigeye thresher (<i>Alopias superciliosus</i>)	12	1	3	25.0	22.6	16.5
Pelagic thresher shark (<i>Alopias pelagicus</i>)	28	0	10	35.7	na	na
Total	308	53	32	10.4	na	na

¹ Sampled for biochemical correlates of morbidity and mortality (Moyes et al., 2006).

² At-vessel mortality estimates of pelagic sharks from the shallow-set longline gear targeting swordfish (*Xiphias gladius*) and deep-set longline gear targeting bigeye tuna (*Thunnus obesus*) in the Hawaii-based longline fishery, 2004–06 (Walsh et al., 2009).

Table 3

Meta-analysis of postrelease mortality of blue sharks (*Prionace glauca*) as determined from pop-up satellite archival tags (PSATs). The postrelease mortality rate estimate was determined with a random-effects model, where each study was assumed to have its own postrelease mortality rate and variance. Details of the analysis can be found in the text and in Borenstein et al. (2009). Nonreporting PSATs were not used in the analysis.

Study	Samples ¹	Postrelease mortality rate	95% confidence interval
Weng et al. (2005)	2/17	0.118	0.030–0.368
Campana et al. (2009b)	7/37	0.189	0.093–0.347
Stevens et al. (2010)	1/8	0.125	0.017–0.537
Musyl et al. (present study)	1/16	0.063	0.009–0.335
Summary effect	11/78	0.150	0.085–0.251

¹ Postrelease mortality in blue sharks (*Prionace glauca*) determined with PSATs over (/) the total number of reporting PSATs for each study

tests were significantly different among daytime and nighttime comparisons (Figs. 3 and 4; Appendices 2 and 3). The dichotomy between coefficients of variability indicates that bigeye threshers are significantly more active at nighttime than during daytime. The aggregated temperature-depth profile (Fig. 4B) and vertical movements indicate that bigeye threshers spend most of their time beneath the uniform temperature surface layer, and that increased variability in vertical movement patterns occurs during crepuscular transitions (Fig. 4E).

Oceanic whitetip sharks and silky sharks showed similar vertical movement patterns (Figs. 5 and 6, respectively), and the depth and temperature data indicated that both species were largely confined to the uniform temperature surface layer (Figs. 3, 5, and 6; Appendices 2 and 3). Although oceanic whitetip sharks and silky sharks exhibited plasticity in their daytime and nighttime vertical movements, both species spent >95% of their time at temperatures that were within

2°C of the uniform temperature surface layer (Table 4). Oceanic whitetip sharks (Fig. 5E) and silky sharks (Fig. 6E) exhibited pronounced movements at crepuscular periods and both species showed significant correlations between average nighttime depths and lunar illumination (Appendix 2).

Further analysis of silky shark data indicated distinct depths and temperatures occupied north and south of 10°N, delimited by the NEC (Fig. 1C). Comparisons of pooled day and night data showed that silky sharks north of 10°N remained significantly deeper (median=54 m, mean=57 m ± 0.4 SE, interquartile range [IQR]=22–86 m) than immature silky sharks south of 10°N (median=32 m, mean=32 m ± 0.3 SE, IQR=11–48 m) (MWBC, $z = -108.9$, Monte Carlo $P < 0.0001$). Likewise silky sharks north of 10°N experienced significantly cooler temperatures (median=25.5°C, mean=25.4°C ± 0.01 SE, IQR=24.7–25.9°C) than silky sharks south of 10°N (median=28.4°C, mean=28.3°C ± 0.007 SE,

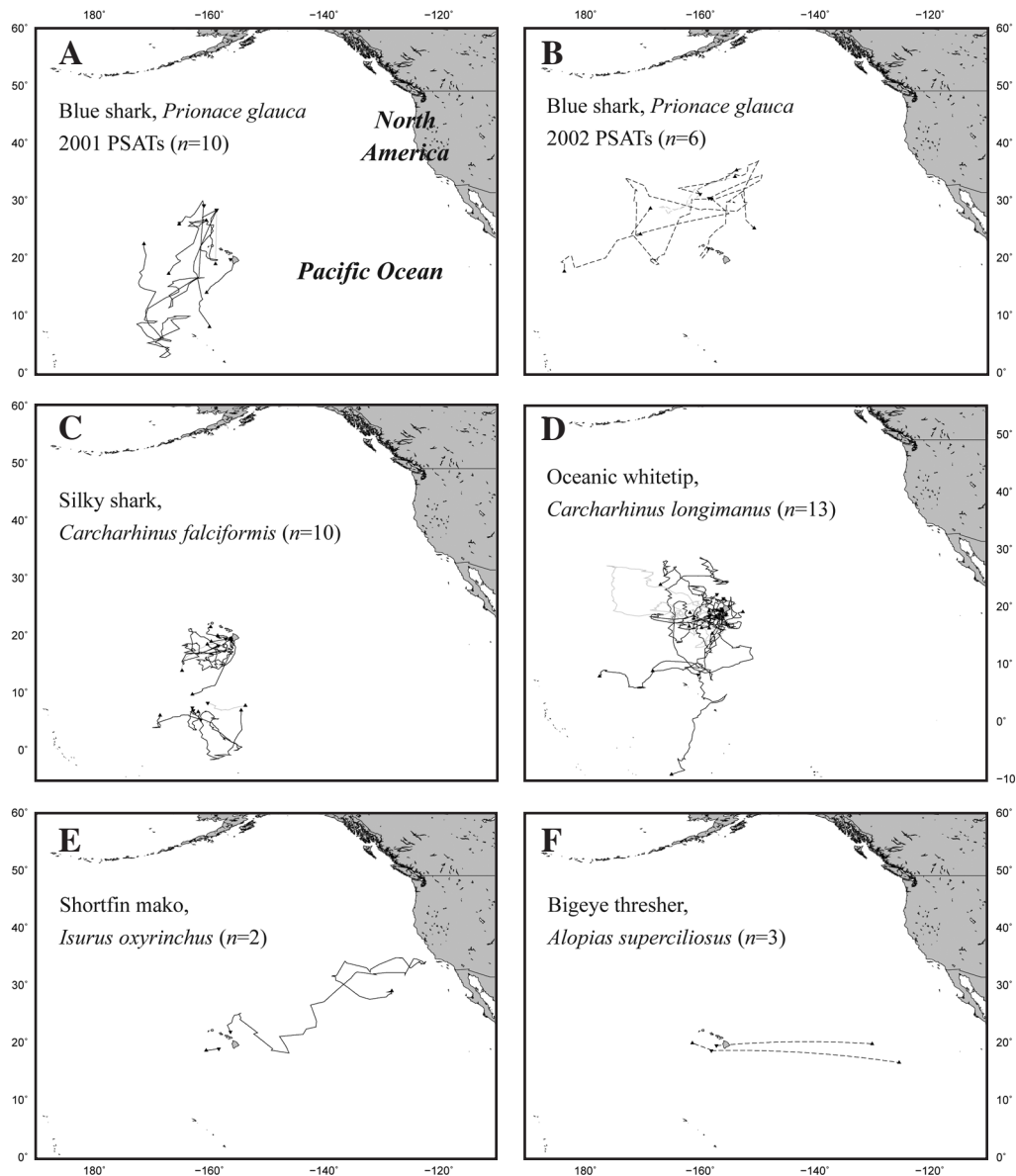
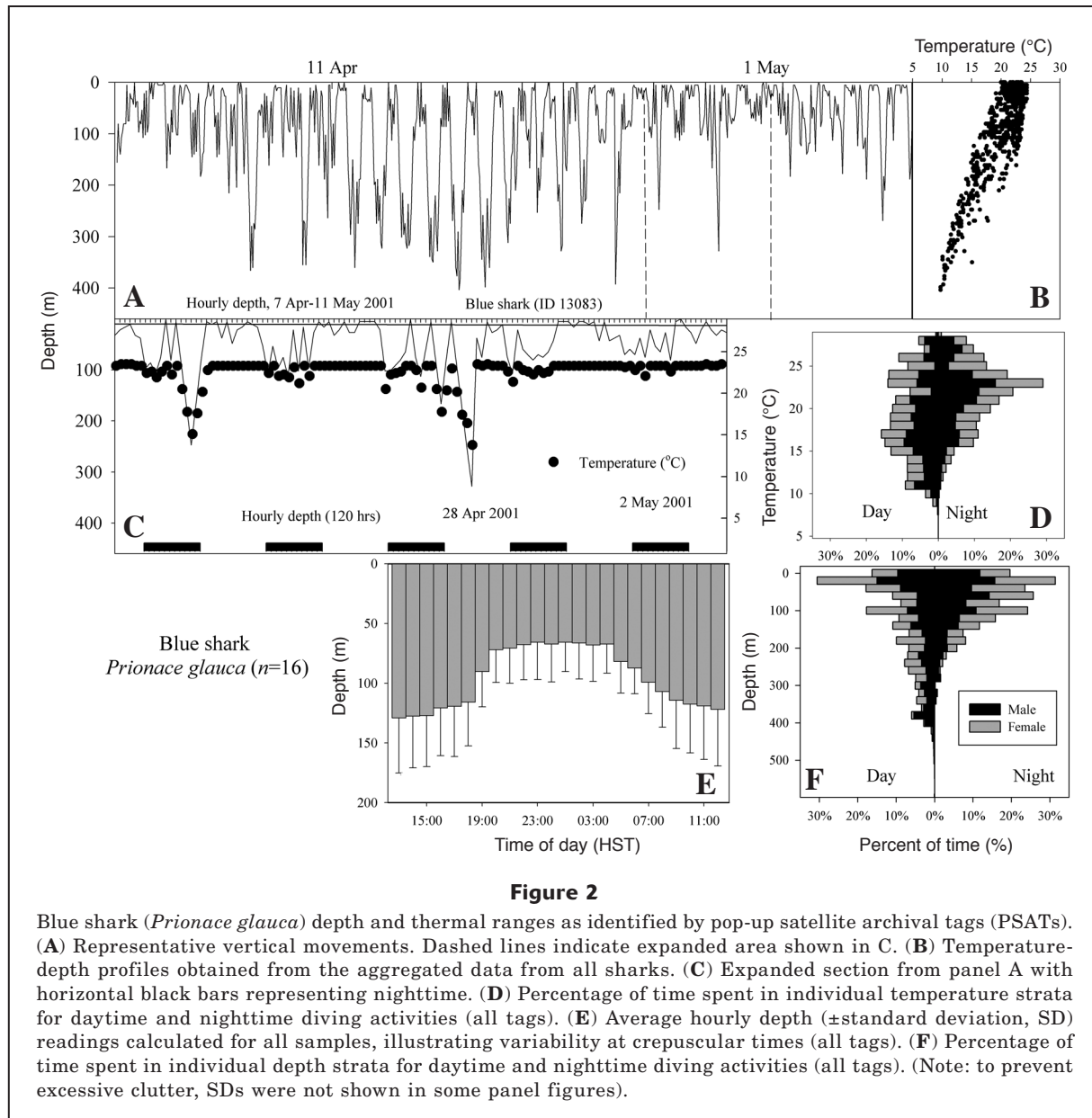


Figure 1

Most probable tracks for five species of pelagic sharks tagged with PSATs and released in the central Pacific Ocean were estimated from the raw geolocations using the Kalman filter-sea surface temperature state-space model (Appendix 1). Downward triangles indicate pop-up satellite archival tag (PSAT) deployment locations and upward triangles indicate PSAT pop-up locations. In situations where no geolocation data were returned, movements of sharks from PSAT deployment to pop-up locations are indicated as a straight line. (A) Blue sharks (*Prionace glauca*) tagged in 2001, where male shark movement patterns are shown in gray; (B) blue sharks (*Prionace glauca*) tagged in 2002, where male shark movement patterns are shown in gray; (C) silky sharks (*Carcharhinus falciformis*), where female movement patterns are shown in gray; (D) oceanic whitetip sharks (*C. longimanus*), where female movement patterns are shown in gray; (E) shortfin makos (*Isurus oxyrinchus*) ($n=2$, both female); and (F) bigeye threshers, (*Alopias superciliosus*).

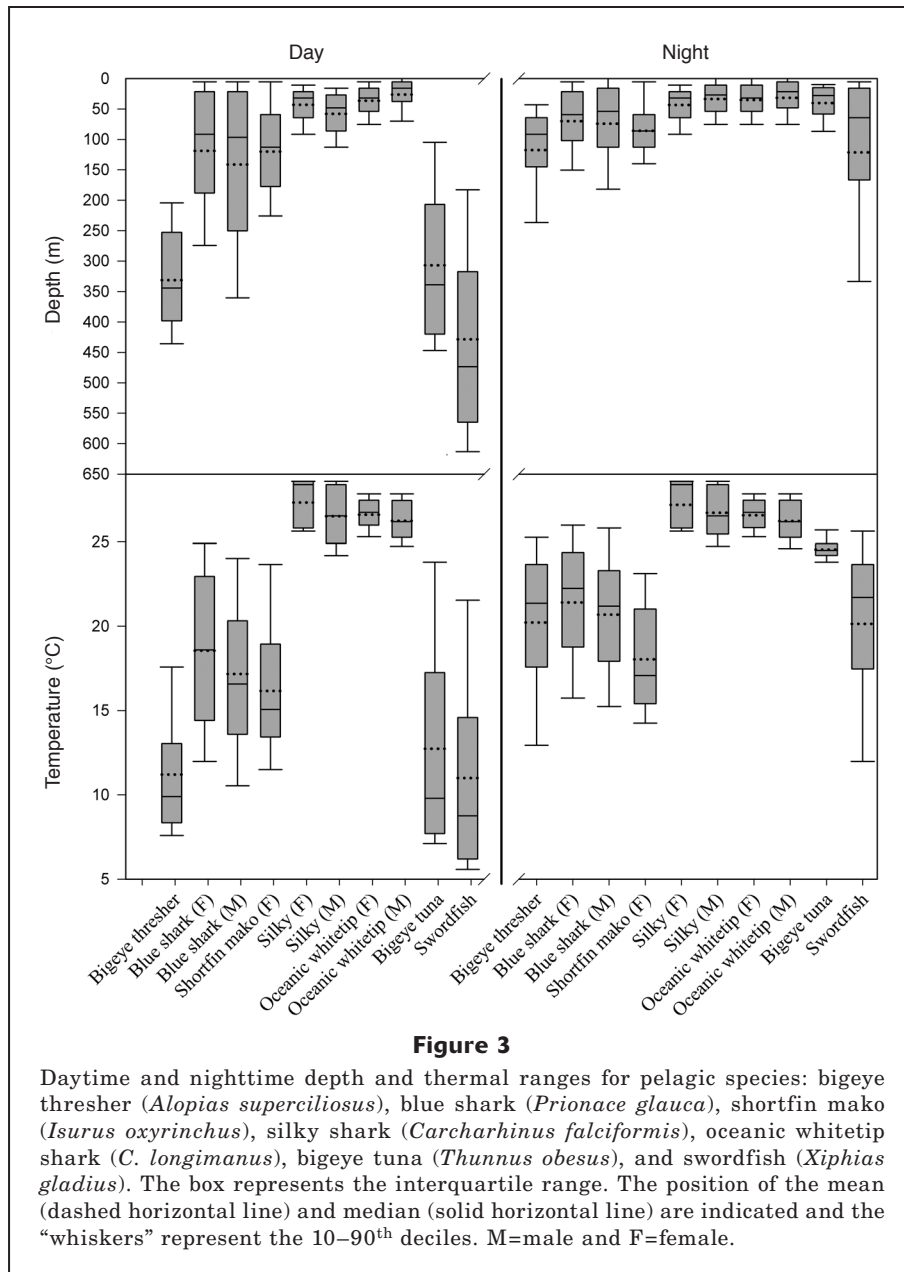
IQR=28.2–28.6°C) (MWBC, $z = -39.47$, Monte Carlo $P < 0.0001$). Within and between these two geographic groups, significantly different trends for depth and temperature preferences during daytime and nighttime were also observed.

Female shortfin makos remained significantly deeper and at cooler temperatures during the daytime than at nighttime (Figs. 3 and 7; Appendices 2 and 3). Unlike pronounced crepuscular patterns exhibited by blue sharks, bigeye threshers, silky sharks, and oceanic



whitetip sharks; shortfin makos did not display striking changes in behavior during crepuscular transitions (Fig. 7E). Traveling west to east from deployment to pop-up location can alter times of sunrise and sunset by as much as -4 and -1.5 h, respectively, but one shortfin mako (ID 38572) made no obvious depth corrections to account for spatial changes in the times of local sunrise and sunset as did bigeye threshers (*cf.* Fig. 4E). Shortfin makos made regular excursions beneath the uniform temperature surface layer, and vertical movement patterns were more variable during daytime than at nighttime (Figs. 3 and 7). Around 27 January 2003, a shortfin mako (ID 38572) crossed the $\sim 18^{\circ}\text{C}$ SST isotherm, the southern boundary of the North Pacific Transition Zone (Polovina et al., 2001),

at 31.34°N , 135.18°W (Fig. 1E) and moved into cooler water. Comparisons of pooled daytime and nighttime data showed that this individual remained significantly deeper (median=113 m, mean=125 m ± 2 SE, IQR=91–161 m) in warmer water than after it crossed the boundary and entered cooler water (median=87 m, mean=90 m ± 2 SE, IQR=39–118 m) (MWBC, $z = -16.45$, Monte Carlo $P < 0.0001$). Temperature data indicated that significantly warmer temperatures were encountered before 27 January 2003 (median=21.02°C, mean=20.5°C ± 0.01 SE, IQR=19–22°C) than after this date (median=14.9°C, mean=14.8°C ± 0.05 SE, IQR=14–16°C) (MWBC, $z = -35.04$, Monte Carlo $P < 0.0001$). The switching between water masses is clearly seen in the temperature-depth profile (Fig. 7B).

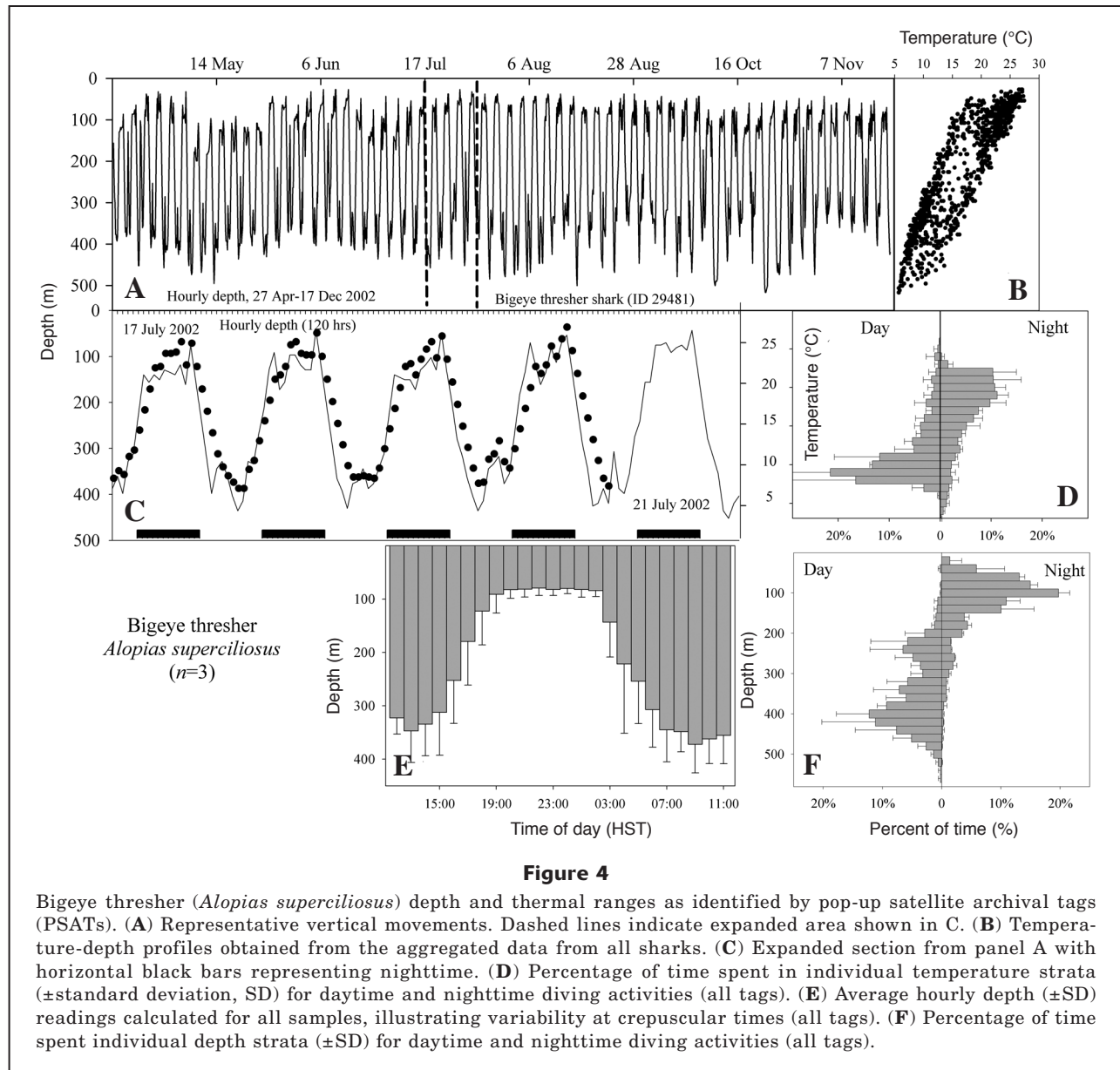


Grouping of vertical movement patterns

Kruskal-Wallis ANOVAs showed that medians of depth and temperature data across individuals for each pelagic shark species (24 total tests) were all significantly different for the six PSAT data streams, indicating substantial amounts of individual variability in vertical movement patterns (Appendix 3). This result was confirmed by *post-hoc* pairwise MWBC tests (Appendix 3). Significantly different daytime and nighttime median depths and temperatures (DD vs. ND, DT vs. NT) were evident in most pooled comparisons (including those by sex) and in the majority of comparisons within and between individuals. Results from two-sample KS tests for each of the

pelagic shark samples paralleled the results given for the MWBC tests. For the entire sample of 394 possible two-sample KS tests in which depth distributions between individuals were compared, 94% of tests were significantly different. And of 394 possible tests for temperature comparisons, 98% of tests were significantly different.

Although individuals exhibited high levels of variability, we were able to partition shark species into three major groups based on daytime temperature preferences by using UPGMA clustering with the D_{\max} distance (Fig. 8). These were 1) epipelagic species that included silky sharks and oceanic whitetip sharks, plus the outgroups black marlin and blue marlin; 2) mesopelagic-I species that included blue sharks and shortfin makos;



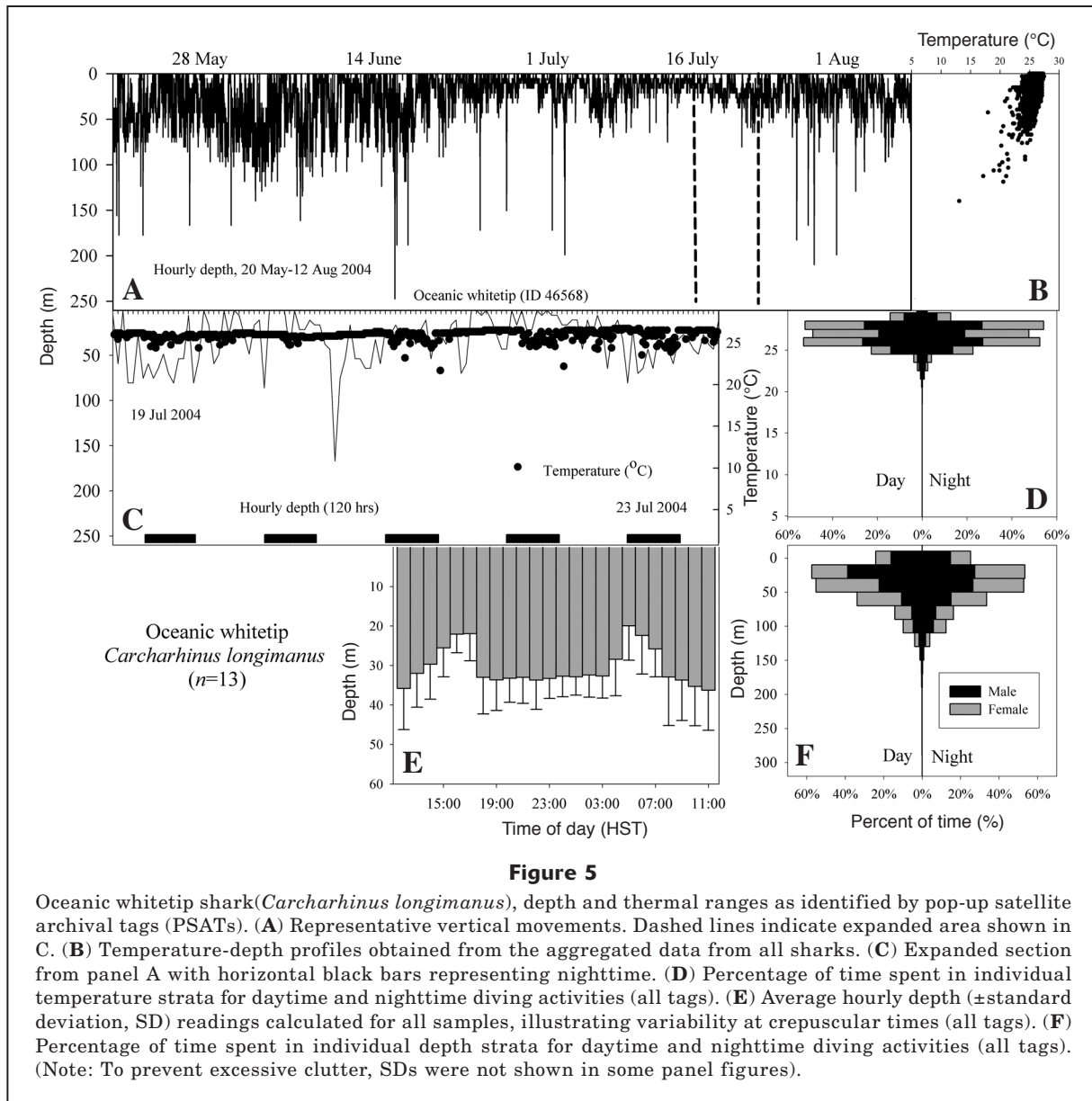
3) mesopelagic-II species that included bigeye threshers plus outgroups bigeye tuna and swordfish. The epipelagic group could be further broken down by body size and latitude because juvenile silky sharks south of 10°N formed the most distinctive cluster (i.e., exhibited the longest branch lengths). Moreover, another distinctive epipelagic cluster was composed entirely of presumably mature silky and oceanic whitetip sharks >200 cm TL whose PSATs separated from the sharks at latitudes above 18°N . The cophenetic correlation (0.86) indicated “good” fit between the data matrix and resultant dendrogram. A similar clustering pattern was obtained with daytime depth data (cophenetic correlation=0.88) but it included five mismatches to the pattern observed with daytime temperature (i.e., black marlin ID 13208, silky shark IDs 38573, 38581, 38601 were placed in

mesopelagic-I and blue shark ID 13095 was placed in the epipelagic group). The mismatches, however, may have been attributable to the relatively poor resolution of PSAT depth data in comparison with the temperature data. There was, however, no discernible pattern with nighttime depth (cophenetic correlation=0.77) and temperature data (cophenetic correlation=0.88) because all species generally remained near the surface.

Discussion

Rates of at-vessel and postrelease mortality

Mortality for blue sharks at the time of gear retrieval in commercial longline fisheries operating in the



Atlantic range from 10–32% (32%, Hoey and Moore¹; 31%, Diaz and Serafy, 2005; 13.2%, Beerkircher et al., 2008; ~10%, Carruthers et al., 2009; 16%, Campana et al., 2009a). By contrast, in central Pacific longline fisheries, Walsh et al. (2009) reported that only 4% and 6% of blue sharks were dead on retrieval from deep-set tuna and shallow-set swordfish gear, respectively. Our sample sizes, except for those for blue sharks, were not large enough to have a strong statistical impact; nevertheless, our estimates of at-vessel mortality appear to be species-specific and correlate with observations for the shallow-set sector of the Hawaii-based longline fishery (Walsh et al., 2009). The at-vessel mortality estimates for blue sharks were also concordant with those reported in the Pacific by Yokota et al. (2006, 2–11%) and Hight et al. (2007, ~6%).

Our reporting rate for PSATs attached to blue sharks (50%) was similar to that reported by Weng et al. (2005) for 28 PSATs (61%, CI*=43–79%). Non-reporting tags, however, cannot be considered synonymous with mortality because other factors can cause failure in electronic tags (Goodyear, 2002; Hays et al., 2007; Campana et al., 2009a; Musyl et al., 2011). PSATs can, however, provide less ambiguous identification of mortality because they will automatically release from the animal at programmed depths (Moyes et al., 2006). This is especially true for sharks because dead sharks are negatively buoyant and sink, thus carrying the PSATs to depths where the pressure-activated release mechanism will be engaged (Moyes et al., 2006; Campana et al., 2009a).

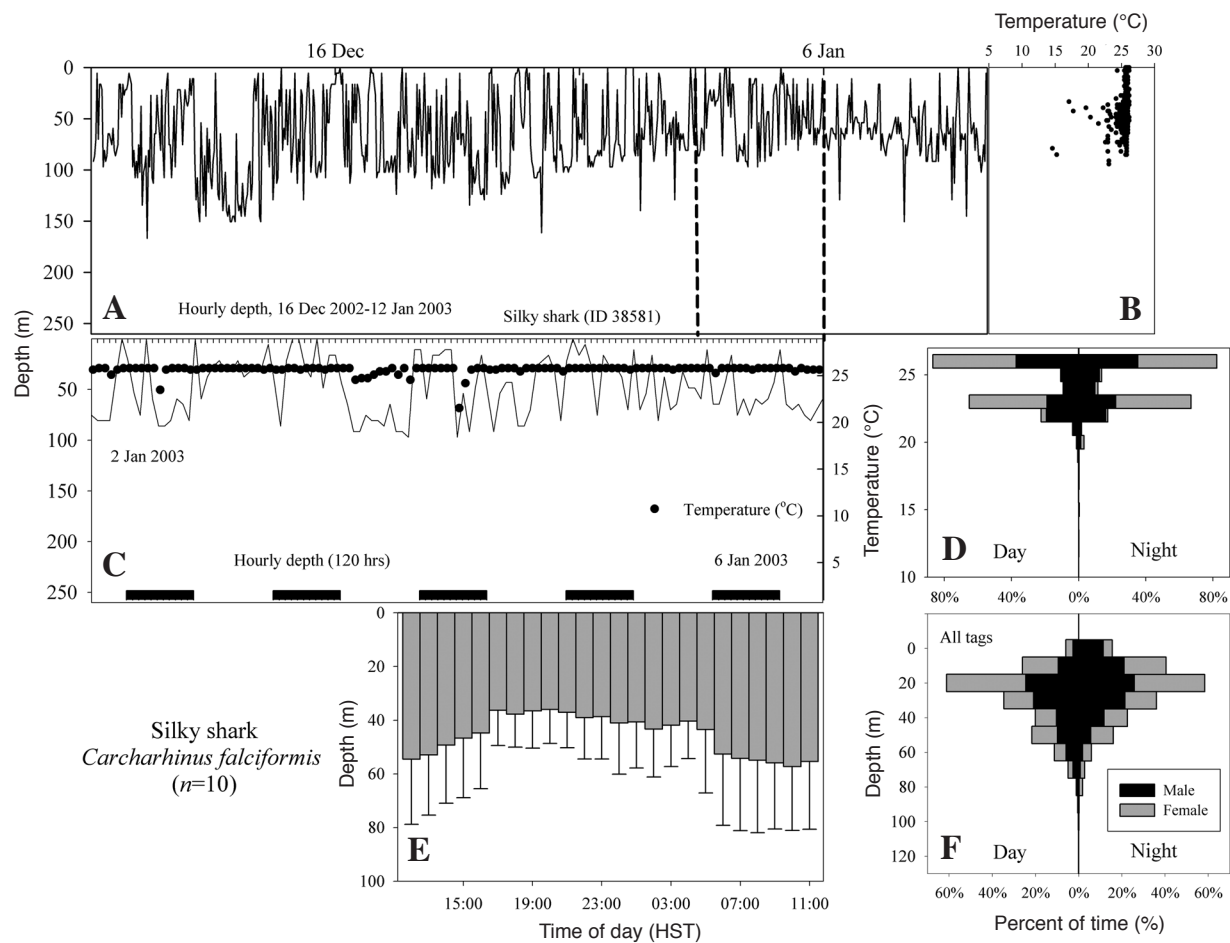


Figure 6

Silky shark (*Carcharhinus falciformis*) depth and thermal habitat as identified by pop-up satellite archival tags (PSATs). (A) Representative vertical movements. Dashed lines indicate expanded area shown in C. (B) Temperature-depth profiles obtained from the aggregated data from all sharks. (C) Expanded section from panel A with horizontal black bars representing nighttime. (D) Percentage of time spent in individual temperature strata for daytime and nighttime diving activities (all tags). (E) Average hourly depth (\pm standard deviation, SD) readings calculated for all samples illustrating variability at crepuscular times (all tags). (F) Percentage of time spent in individual depth strata for daytime and nighttime diving activities (all tags). (Note: To prevent excessive clutter, SDs were not shown in some panel figures).

Campana et al. (2009a), using PSATs, determined that 19% (CI*=8–32%) of blue sharks tagged in the North Atlantic longline fishery targeting swordfish and released alive subsequently died. We could find only two other published studies where PSATs had been used with blue sharks and that provided postrelease mortality estimates. Weng et al. (2005) and Stevens et al. (2010) reported 11.8% (CI*=0–29%) and 14.3% (CI*=0–42%) postrelease mortality, respectively. As determined by meta-analysis with all available data from 78 reporting PSATs, the summary effect of postrelease mortality of blue sharks was 15% (95% CI, 8.5–25.1%). However, because only two of four studies were specifically designed to estimate mortality, experimental bias could be a confounding

factor, as well as small and unrepresentative sample sizes (Campana et al., 2009b; Musyl et al., 2009).

We could find no equivalent postrelease mortality estimates for bigeye thresher, shortfin mako, silky sharks, or oceanic whitetip sharks. Heberer et al. (2010), using PSATs, reported a 26% postrelease mortality rate of common thresher sharks released from recreational gear where fight-times ≥ 85 minutes identified survivors from moribund individuals. Our postrelease mortality rates for pelagic sharks were similar to PSAT tagged istiophorid billfish released from commercial pelagic longline gear in the Atlantic (average postrelease mortality rate was 9%, CI*=2–18%) (Kerstetter et al., 2003; Kerstetter and Graves, 2005, 2008).

Table 4

Cumulative percentage of temperature readings from pop-up satellite archival tags (PSATs) attached to silky and oceanic whitetip sharks expressed as differences from daily calculated sea surface temperature (Δ SST°C) for daytime and nighttime diving behavior.

Silky shark (*Carcharhinus falciformis*)

Day	52.56	87.06	95.78	98.26	99.53	99.84	99.96	100	
Night	63.30	91.63	96.93	98.80	99.26	99.48	99.71	99.83	100
Total	57.71	89.25	96.33	98.52	99.40	99.66	99.84	99.92	100
Δ SST (°C)	0	-1	-2	-3	-4	-5	-6	-7	-8

Oceanic whitetip shark (*Carcharhinus longimanus*)

Day	63.89	91.53	96.88	98.59	99.36	99.63	99.87	99.95	100
Night	61.40	89.98	95.92	98.39	99.21	99.58	99.86	99.94	100
Total	62.67	90.77	96.41	98.49	99.29	99.61	99.86	99.95	100

Methods for determining postrelease mortality in large pelagic fishes and sharks

Implementing survival studies for pelagic species is challenging because of logistics, cost, experimental design, and obtaining sufficient samples. There are only a few methods for estimating survival, and each has limitations. Historically, long-term survival of pelagic species has been estimated by large-scale conventional tagging programs with low return rates (<5%, blue shark, Kohler et al., 1998; ~1%, blue marlin, Ortiz et al., 2003). Such results are consistent with a high postrelease mortality but could also be attributed to large population sizes, dispersal, tag loss, or uncooperative fishermen. Direct observation in tank or pen studies (e.g., Mandelman and Farrington, 2007) may not be practical for large pelagic species. Although they are the right tool to indicate postrelease mortality, the cost of PSATs precludes their widespread application. Moyes et al. (2006) introduced a biochemical approach that reduces experimental bias and increases sample size and would therefore optimize experimental design. Once the method is operational, about 40 samples can be assayed for the cost of one PSAT (~US\$ 4000) (Musyl et al., 2009). Other potential methods that could achieve sufficient sample sizes have shown promise for other species (e.g., reflex action mortality predictors; Davis, 2007), but it is not known how well these methods would translate for large pelagic species. For example, we used the absence of movement in the nictitating membrane to determine at-vessel mortality, but it is not known whether variability in this response (or other responses) would be useful to predict postrelease mortality. Lastly, bioelectrical impedance analysis (Cox and Heintz, 2009) may be feasible if body condition correlates with long-term survival.

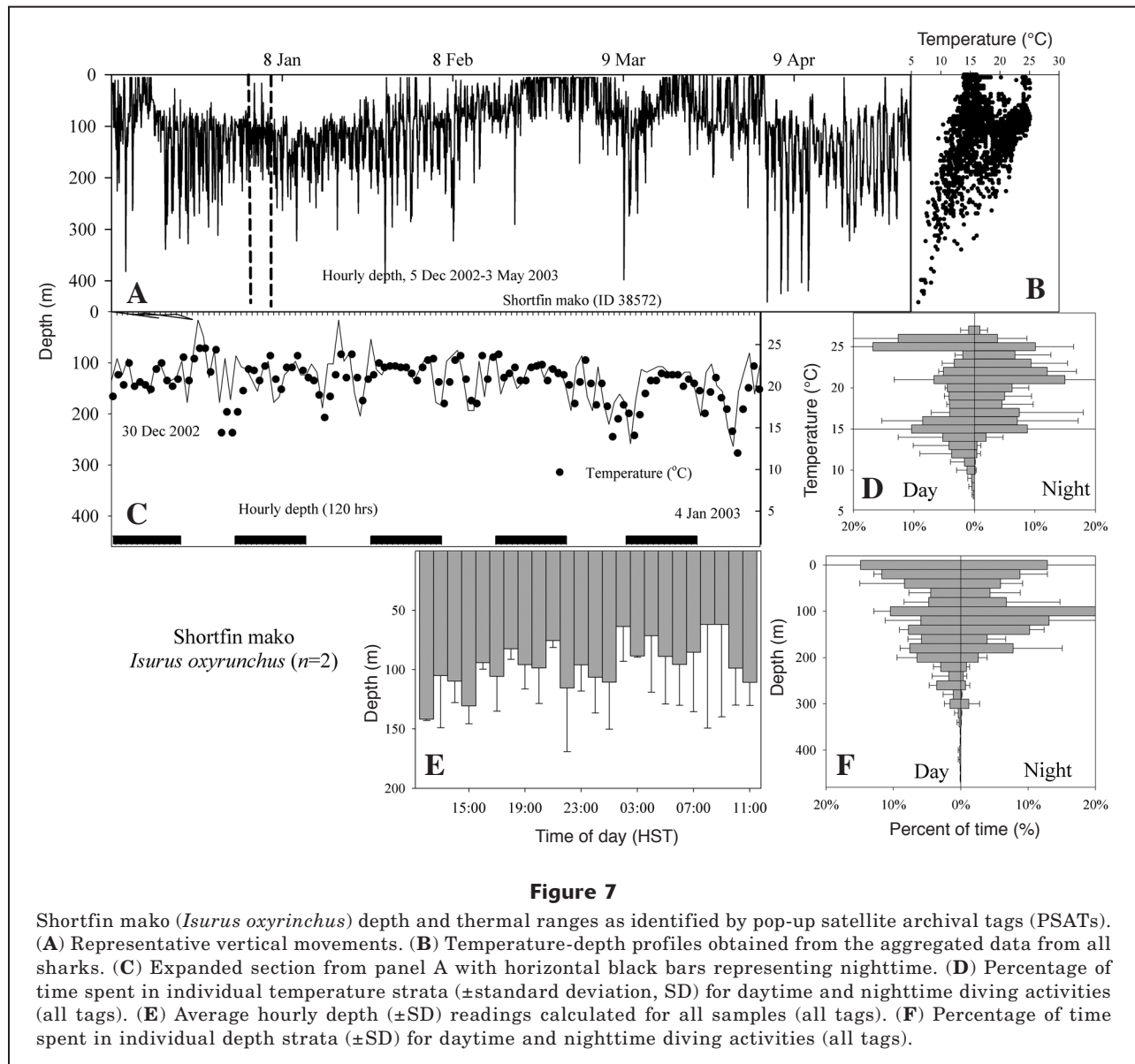
Factors that influence mortality

Presumably the effects of stress and injury during capture are additive and unless there are overriding factors,

we suggest that, under similar conditions (and with adequate sample sizes), the at-vessel and postrelease mortality rates for pelagic species should be roughly concordant (e.g., Moyes et al., 2006; Campana et al., 2009a). For survival studies on blue sharks, the at-vessel and postrelease mortality estimates show close agreement. For example, Campana et al. (2009a) reported 16% at-vessel and 19% postrelease mortality rates and we reported 5.9% at-vessel and 6.3% postrelease mortality rates. Although we did not find this relationship for other pelagic sharks, it is possible our sample sizes were not sufficient to detect differences between these two mortality rates.

Clearly additional research is required to determine whether at-vessel mortality correlates with postrelease mortality across a range of shark species and to determine which biological and anthropogenic factors account for variability in mortality estimates. As discussed in Musyl et al. (2009), postrelease mortality estimates in Campana et al. (2009a) may have been strongly influenced by handling. Hoey and Moore¹ suggested that a 20% difference in mortality for blue sharks discarded from longlines was attributable to handling practices in the Atlantic fishery where the Campana et al. (2009a) study took place. Campana et al. (2009a) also reported a significant vessel effect in their survival model of retrieved dead sharks, which the authors attributed to handling. Carruthers et al. (2009) and Diaz and Serafy (2005) also suggested discard and handling practices may have been responsible for differences in at-vessel mortality rates of blue sharks in the Atlantic longline fishery. If differences in handling practices strongly correlate with variable survival, a logical extension would be to develop discard-and-release regulations that could significantly improve survival (Carruthers et al., 2009).

Circle hooks were used throughout our study which probably increased both the at-vessel survival (Diaz and Serafy, 2005; Kerstetter and Graves, 2006; Campana et al., 2009a; Carruthers et al., 2009; Musyl et al., 2009) and postrelease survival of blue sharks (Moyes



et al. 2006; Campana et al., 2009a; Musyl et al., 2009) captured and released from longline gear. Similar findings have been reported for istiophorid billfish, which showed significantly lower at-vessel mortality (Diaz, 2008; Serafy et al., 2008) and postrelease mortality (Horodysky and Graves, 2005) with the use of circle hooks over J-hooks. Campana et al. (2009a; 2009b) did not mention the hook type used on blue shark that ultimately died when released from commercial longline gear. However, we argue that given their observed rates of at-vessel mortality, it is likely that this factor, along with handling and time spent hooked, were important factors to explain their rates of postrelease mortality (Musyl et al., 2009).

The amount of time spent on the hook shows a positive relationship with mortality for a variety of pelagic

species, presumably because the captured animal experiences increased stress over time and is more vulnerable to predation (Boggs, 1992; Erickson and Berkeley, 2008; Carruthers et al., 2009). Many authors suggested that shorter soak times could significantly reduce bycatch mortality (Diaz and Serafy, 2005; Erickson and Berkeley, 2008; Carruthers et al., 2009). Without the benefit of hook timers (Boggs, 1992; Erickson and Berkeley, 2008) however, it would be challenging to test the correlation between time spent on the line and mortality. Our samples probably consisted of both mature and immature sharks, but we could not determine any significant trends between mortality and size as reported in Diaz and Serafy (2005).

Lastly, we also observed species-specific differences in the at-vessel mortality rates which other authors

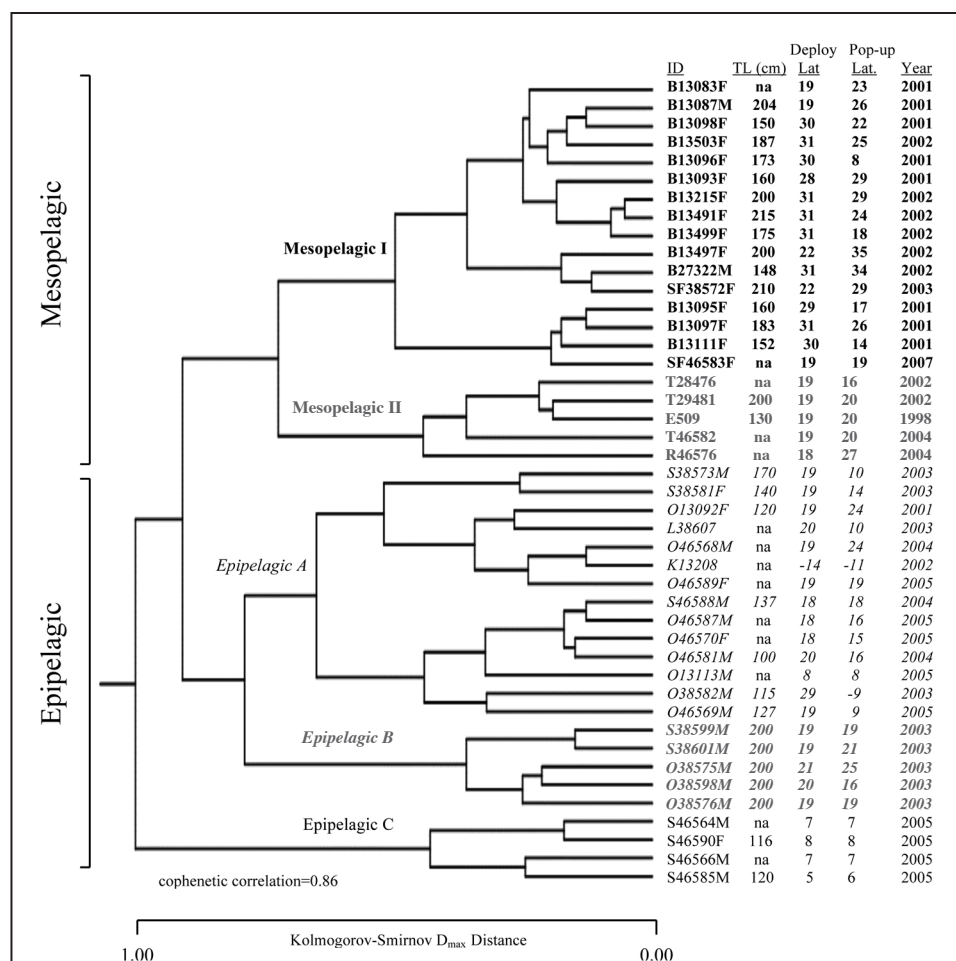


Figure 8

Dendrogram of epipelagic and mesopelagic species clusterings for five species of sharks, determined with unweighted pair-group method using arithmetic averages (UPGMA) and daytime temperature preference readings from pop-up satellite tags (PSATs). ID abbreviations: B=blue shark (*Prionace glauca*), SF=shortfin mako (*Isurus paucus*), T=bigeye thresher (*Alopias superciliosus*), E=bigeye tuna (*Thunnus obesus*), R=swordfish (*Xiphias gladius*), S=silky shark (*Carcharhinus falciformis*), O=oceanic whitetip shark (*C. longimanus*), K=black marlin (*Istiompax indica*), L=blue marlin (*Makaira nigricans*), M=male, and F=female, TL=total length (cm) and PSAT deployment and pop-up latitude are provided with pop-up year. na=not available. Outgroup data were taken from Pacific swordfish, black marlin, blue marlin (Musyl et al.²) and bigeye tuna (Musyl et al., 2003). Italic and bold fonts are used to distinguish the various species groupings.

have noted (e.g., Hight et al., 2007; Erickson and Berkeley, 2008; Walsh et al., 2009), presumably because of species-specific tolerances to stress and injuries (Hight et al., 2007; Mandelman et al., 2008; Mandelman and Skomal, 2009). For example, in the Pacific, Hight et al. (2007) reported blue sharks to exhibit significantly lower catecholamine levels than shortfin makos during retrieval of longline gear. The difference agrees with results indicating much lower at-vessel mortality for blue sharks (Walsh et al., 2009).

Species-specific vertical and horizontal movements

Our results strongly indicate that pelagic sharks exhibit high levels of individual variability in their vertical movement patterns and these are significantly influenced by time of day, and the transitions from daytime to nighttime diving activity can be dramatic. Plasticity in diel vertical movement patterns has also been documented in bigeye tuna (Musyl et al., 2003) and southern bluefin tuna (*T. maccoyii*, Bestly et al., 2009) and other pelagic species (Arnold and Dewar, 2001; Gunn and

Block, 2001). Our data also indicate that vertical mobility patterns are species-specific. Moreover, the vertical movement patterns of bigeye thresher and blue sharks and shortfin makos appear to allow them to remain in the vicinity of prey organisms in the deep sound scattering layer (SSL), as is the case for swordfish and bigeye tuna (Childress and Nygaard, 1974; Carey, 1990; Josse et al., 1998; Musyl et al., 2003, Musyl et al.²), during their extensive daytime vertical migrations, with additional adjustment of nighttime vertical movement behaviors to lunar illumination (e.g., Musyl et al., 2003). By contrast, the epipelagic silky and oceanic whitetip sharks remain in the upper mixed layer (~120 m) both night and day. Diet studies (Tricas, 1979; Harvey, 1989; Preti et al., 2008) and observations from submersibles (Davies and Bradley, 1972) indicate overlap among pelagic shark species which are in concordance with the overlap in diel vertical movement patterns, especially at nighttime when species remain near the surface.

With the exception of shortfin makos, the pelagic sharks in our study displayed distinct changes in vertical movement patterns during crepuscular transitions. Pronounced or regular activity at crepuscular periods has been hypothesized to aid in orientation and navigation (e.g., by detecting sun angles and geomagnetic or electric fields; Carey and Scharold, 1990; Musyl et al., 2001, 2003; Klimley et al., 2002; Willis et al., 2009). Other authors have suggested this strategy reflects movements of the organisms of the SSL (Josse et al., 1998; Musyl et al., 2003). Klimley et al. (2002) postulated that shortfin makos occasionally dive deep to sample magnetic gradients, but also need to sample the earth's main dipole field at the surface where it is strongest. The absence of pronounced vertical movements during crepuscular transitions indicates sun elevations or changes in light-intensity may not be critical for navigation.

Examining data from 22 blue sharks carrying ultrasonic transmitters, Carey and Scharold (1990) noted the largest vertical oscillations during the day (descents to 620 m and 7°C) and smaller excursions at night. Blue sharks appear to have no unique anatomical or physiological adaptations (e.g., thermoconserving mechanisms necessary for regional endothermy) and Carey and Scharold (1990) suggested this "up and down movement" pattern might be a hunting tactic, behavioral thermoregulation, or an efficient way to sample odor plumes that tend to spread horizontally throughout the water column. Lastly, divergent vertical movement behaviors could be specific search behaviors tailored to finding the availability of specific resources (Sims et al., 2008; Humphries et al., 2010). For example, when resources are scarce and patchily distributed, pelagic sharks adopt a Lévy flight behavior, but at thermal fronts, where there are abundant resources, they switch to Brownian movement (Humphries et al., 2010).

PSAT data from blue sharks in eastern Australia have shown diel vertical movement patterns (i.e., deeper in daytime and near the surface at nighttime) with

the majority of the time spent between 17° and 20°C and approximately 80% of vertical movements above ~200 m, but maximum depths reached may have been constrained by bathymetry (Stevens et al., 2010). In contrast, blue sharks in our study experienced a larger range in temperatures (e.g., 80% of temperatures occupied were from 13–26°C) as a result of their greater vertical mobility. In the tropical Indian Ocean, catch data indicated the abundance of blue sharks was greatest at depths of 80–220 m and at temperatures from 12° to 25°C (Compagno, 1984)—data that correlate with our results. Nakano et al. (1985) offered that 14–21°C was the preferred temperature of blue sharks in the North Pacific, whereas Strasburg (1958) claimed that 99% of the blue shark catch in the Pacific was taken by long-line hooks in waters between 7° and 20.5°C—hooks that were in or immediately below the thermocline.

The horizontal movements of blue sharks that we observed generally followed the seasonal and ontogenetic north–south migratory patterns reported by Strasburg (1958) and Nakano and Stevens (2008). Weng et al. (2005) reported movements of blue sharks from the eastern Pacific into the central Pacific, but it is unclear if populations of blue sharks in the central Pacific are regularly supplemented by recruits from the eastern Pacific. Moreover, to our knowledge, movements of blue sharks from the central to eastern Pacific have not been documented. Understanding these movement patterns would be helpful for stock assessments.

Apart from anecdotal and taxonomic information (Compagno, 1984; Bonfil et al., 2008) very little data exist about the life history and ecological requirements of oceanic whitetip sharks. The movement data reported herein are in agreement with published summaries on the biology of this species (Bonfil et al., 2008), which generally indicate their habitat to be primarily in the uniform temperature surface layer. We found that oceanic whitetip sharks spend >95% of their time at temperatures within 2°C of SST. Strasburg (1958) concluded that the whitetip "was surface dwelling north of the equator and bathypelagic to the south," whereas Compagno (1984) suggested that this species can tolerate temperatures from 18° to 28°C but normally prefers water above 20°C. Bonfil et al. (2008) suggested that blue and oceanic whitetip sharks—the most abundant oceanic sharks—have evolved an efficient partitioning of the oceanic environment," and our data clearly support this conclusion.

Silky sharks have been reported to be limited to water temperature >23°C (Last and Stevens, 2009) which agrees with our data. Compagno (1984), however, suggested that silky sharks could inhabit depths below 500 m, something we did not observe. Watson et al. (2009) reported finding smaller, immature silky sharks captured by purse seine north of the equator in the eastern tropical Pacific. In our cluster analysis, the most unique cluster was composed of immature silky sharks south of the NEC, and silky sharks segregated by body size and also by latitude. Presumably this topology is temporary and changes through ontogeny.

The most striking diel vertical movement behavior among pelagic shark species was observed in bigeye threshers. Our observations were similar to those of Nakano et al. (2003) who acoustically tracked two immature females (175 and 124 cm precaudal length) for 96 and 70 h, respectively; their vertical movements were centered between 200 and 500 m during the day and 80 and 130 m at night. Moreover, the diel vertical movement patterns we observed were comparable to the PSAT data reported by Weng and Block (2004).

Movement data of the shortfin makos that we observed were similar to those recorded by Loefer et al. (2005) for this species in the Atlantic, in that both studies recorded adjustment of vertical behavior when the sharks entered water masses with different thermal characteristics. However, shortfin makos in the Atlantic made excursions from the surface to 556 m (temperatures from 10.4° to 28.6°C), whereas we never observed movements below ~441 m.

Thermal niche partitions and habitat structure

Our results show that pelagic shark species display distinct thermal niche partitioning (as identified by UPGMA clustering) and that habitat structure for the epipelagic silky and oceanic whitetip sharks can be adequately estimated from two dimensions (these species spend most of their time in the warmest available water). By contrast, three dimensions will be required to describe the extended vertical habitat of the species that we classified as mesopelagic I (blue sharks, shortfin makos) and mesopelagic II (bigeye threshers).

Except for the oceanic whitetip shark and silky shark clusters, which showed familial affinities based on phylogeny and life history, the topology of the dendrogram for pelagic shark species appeared to correlate with body size and latitudinal gradient, but not with phylogeny (Shirai, 1996), life history (Cortés, 2000), ecomorphotype (Compagno, 1990), neural anatomy (Lisney and Collin, 2006; Yopak and Montgomery, 2008; Yopak and Frank, 2009), relative eye size (Lisney and Collin, 2007), or the presence of regional endothermy (Bernal et al., 2001; Dickson and Graham, 2004). It also does not appear that clustering was greatly influenced by the El Niño-Southern Oscillation (www.esrl.noaa.gov/psd/people/klaus.wolter/MEI/, accessed November 2010) or Pacific Decadal Oscillation (cses.washington.edu/cig/pnwc/compensopdo.shtml, accessed November 2010) climate patterns.

Dickson and Graham (2004) argued that endothermy *per se* was not required for niche expansion and that other adaptations were necessary to allow for vertical movements below the thermocline. This hypothesis implies that other factors (e.g., ontogeny, latitude, locomotion, diet, and dimensionality of the environment) probably influence thermal niche partitions (Yopak and Montgomery, 2008; Yopak and Frank, 2009). Dietary studies based on accumulation of mercury in prey items, which is depth-dependent, have revealed vertical niche preferences among pelagic species (Choy et al., 2009).

Dagorn et al. (2000) suggested, on the basis of their simulation model, that “different solutions for exploiting the same environment” had evolved among tropical pelagic species; their findings reflected a diverse array of species-specific vertical movement patterns and vertical niche partitions similar to those observed in our study on pelagic sharks. Numerous authors (e.g., Brill et al., 2005; Bernal et al., 2009; Musyl et al.²; and others) have suggested that evolution of the ability to make extensive daily vertical movements in pelagic species may have arisen from predator-prey dynamics. In other words, predator and prey may be locked in a physiological race driving the biological and physiological adaptations and tolerances of both and thus expanding their vertical niche.

For comparative purposes, shark species from other locations could be analyzed with our clustering methods to determine thermal niche clusters. From a practical standpoint, pelagic shark species that form thermal clusters may also experience similar fishing pressures and this association may have direct application to mitigating bycatch. For example, from longline catch data in the Atlantic, Rey and Muñoz-Chapuli (1992) calculated that blue sharks were more likely to be captured in association with shortfin makos rather than with bigeye threshers and this calculation supported our groupings in the cluster analysis.

Conclusions

Results from PSAT tagging indicate that pelagic shark species can have high survival rates when released alive from longline fishing gear, and therefore catch-and-release may be a viable option to protect parental biomass in this fishery. Additional research is warranted to determine which biological and anthropogenic factors correlate with at-vessel and postrelease survival. Furthermore, information on the temporal and spatial vertical distribution patterns and community structure of pelagic species can assist in the formulation of management strategies to modify fishing gear, and thus reduce bycatch. This information should also provide more confidence in predicting catch rates and the species captured in different gear types by managers regulating fishing practices. As the tools and techniques for differentiating postrelease mortality become more refined allowing for larger sample sizes, it should be feasible to design fishing methods and practices that significantly reduce bycatch mortality.

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Appendix 1

Movement parameter estimates for tagged sharks determined from the Kalman filter (KF)-sea surface temperature (SST) state-space model (Nielsen et al., 2006). Blank spaces indicate models in which the parameters were set to zero, i.e., have no influence on the model, and were not estimated. u and v are advection parameters in longitude and latitude, respectively; D=all estimated diffusive parameters, b_x , b_{y0} , b_{sst} are the bias estimates for longitude, latitude and SST, respectively; σ_x , σ_{y0} , σ_{sst} are the standard deviations, a_0 is the upper bound for the latitude variance, b_0 is the estimated number of days before the equinox (when latitude error is maximal), and nlogL is the log-likelihood function. u and v are expressed in nautical mile (nmi) day⁻¹, D in nmi² day⁻¹, b_x , b_{y0} , b_{sst} , σ_x , σ_{y0} , and σ_{sst} in degrees, and a_0 and b_0 in days. Numbers in parentheses after pop-up satellite archival tag (PSAT) no. are number of days with geolocations with M=male, F=female.

PSAT no.	u	v	D	b_x	b_{y0}	b_{sst}	σ_x	σ_{y0}	σ_{sst}	a_0	b_0	nlogL
Blue shark												
<i>(Prionace glauca)</i>												
13087M (9)			949.50				4.57	100	0.09			166.51
13093F (43)			1285.63				3.37	2.65	0.49	0.07	52.3	332.34
13095F (13)			916.80				0.76	10.41	0.36			91.69
13096F (13)	-0.75	-19.70	759.08				2.18	7.01	2.32			109.13
13097F (41)			539.67				1.90	5.29	0.31			282.71
13098F (98)			2990.00			-11.76	2.50	8.73	3.91			1099.83
13111F (18)			480.75				3.54	7.27	1.05			186.23
13215F (26)			1567.10				0.95	3.07	2.27			259.22
13491F (28)			1373.44				1.26	3.83	0.49			260.59
13497F (6)			785.47				0	2.40	1.26			76.48
13499F (11)			1204.47				1.56	5.32				72.60
13503F (17)			698.28				0.79	2.70	0.38			141.51
27322M (36)			582.41				1.97	4.24				198.50
Shortfin mako												
<i>(Isurus oxyrinchus)</i>												
38572F (77)	9.23	3.84	1483.27				0.78	3.57	0.28	0.36	-41.58	708.59
Silky shark												
<i>(Carcharhinus falciformis)</i>												
38573M (87)	-2.74	-3.54	602.29				0.51	2.13	0.16	0.02	-18.54	508.62
38581F (25)	-12.4	-11.8	165.58				0.9	2.13	0.46			140.68
38599M (31)			265.48				0.62	2.93	0.18			169.64
38601M (185)			119.16				0.61	4.46	2.45		-0.89	1573.87
46564M (20)			624.34				0.59	5.91	0.61			163.68
46566M (25)			2357.41				0.48	4.07	0.91			274.26
46571M (8)			105.30				0.26	1.99	0.53			80.79
46585M (91)	-3.70	4.25	701.27				0.73	3.43	0.59	0.02	-0.69	859.75
46588M (91)			791.38				0.42	1.33	0.38		1.03	821.53
46590F (23)			451.12				0.73	5.10	1.30			203.05
Oceanic whitetip shark												
<i>(Carcharhinus longimanus)</i>												
13092F (62)			351.17				1.10	3.26	0.40			510.81
13113M (123)	-5.75	-0.37	358.36				0.97	4.34	0.76		1.28	1170.24
29918F (8)			413.89				0.23	2.47	0.12			58.93
38575M (200)			554.91				0.39	1.98	2.15		2.14	1416.63
38576M (102)			471.92				0.47	1.42	0.22	0.05	-8.24	523.42
38582M (87)	-6.22	-17.05	596.56				0.53	3.82	0.15			372.53
38598M (51)			750.42				0.19	1.33	0.14	0.02	4.35	169.85
46568M (80)	-6.89	2.74	427.95			0.53	0.52	2.08	0.29	0.35	37.74	565.44
46569M (40)			571.16			0.12	0.57	3.88	0.01		-2.59	383.19
46570F (182)			377.06				0.48	8.95	0.36			1605.19
46581M (173)			760.70				0.48	2.35	0.39		0.42	1214.86
46587M (196)			532.79				0.58	3.06	0.37		-3.57	1569.85
46589F (175)			453.52				0.76	2.27	0.30		-1.84	1614.75

Appendix 2

Descriptive statistics of daytime and nighttime vertical movement behavior of blue shark (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*), silky shark (*Carcharhinus falciiformis*), oceanic whitetip shark (*C. longimanus*) and bigeye thresher (*Alopias superciliosus*) tagged with pop-up satellite archival tags (PSATs). For sharks experiencing several lunar cycles, the correlation coefficient (R) is given between average nighttime depth (m) and lunar illumination, where $*P<0.05$; $**P<0.01$; $***P<0.001$. CV is the coefficient of variation, SE is the standard error, and M=mean, F=female. The following percentages of PSAT data were received for each species based on days-at-liberty and data acquisition interval: blue shark; depth (48%), temperature (49%); shortfin mako; depth (38%), temperature (38%); silky shark, depth (50%), temperature (55%); oceanic whitetip shark, depth (53%), temperature (48%); bigeye thresher, depth (18%), temperature (19%).

PSAT no. and sex	Day depth (m)				Night depth (m)				Day temperature (°C)				Night temperature (°C)			
	Mean ±SE	Min-max	CV		Mean ±SE	Min-max	CV		Mean ±SE	Min-max	CV		Mean ±SE	Min-max	CV	
Blue shark (<i>Prionace glauca</i>)																
13081F	209 ±41	81–323	0.44						18 ±1	14–23	0.17					
13083F	108 ±6	0–403	1.04		66 ±3	0–274	0.82		19 ±0	10–24	0.23		22 ±0	13–24	0.10	
13087M	124 ±9	0–371	0.82		97 ±6	0–280	0.71		20 ±0	11–28	0.21		22 ±0	14–28	0.15	
13093F	65 ±3	0–398	1.17		38 ±2	0–307	1.22		18 ±0	8–29	0.25		19 ±0	10–28	0.22	
13095F	61 ±5	0–403	1.38		81 ±3	0–323	0.68		22 ±0	9–26	0.17		22 ±0	11–26	0.11	
13096F	160 ±8	0–522	0.92		93 ±4	0–479	0.91		19 ±0	7–28	0.33		22 ±0	8–28	0.20	
13097F	98 ±3	5–430	0.93		81 ±2	5–317	0.71		22 ±0	9–27	0.17		23 ±0	12–27	0.10	
13098F	73 ±2	0–178	0.76		103 ±1	0–178	0.47		19 ±0	8–29	0.26		23 ±0	10–29	0.17	
13111F	124 ±7	0–581	0.77		119 ±4	0–296	0.49		21 ±0	8–26	0.18		22 ±0	14–26	0.13	
13215F	176 ±3	5–581	0.58		65 ±1	5–344	0.71		17 ±0	5–28	0.29		21 ±0	8–27	0.21	
13491F	149 ±2	0–479	0.70		54 ±1	0–328	0.97		17 ±0	6–29	0.28		21 ±0	9–28	0.20	
13497F	110 ±4	0–350	0.85		46 ±2	0–247	0.92		16 ±0	9–22	0.17		18 ±0	12–22	0.10	
13499F	130 ±11	0–317	0.63		72 ±10	0–225	0.97		18 ±1	9–29	0.3		22 ±0	14–29	0.19	
13503F	92 ±3	0–403	1		55 ±2	0–296	1		19 ±0	9–26	0		20 ±0	10–26	0	
27322M	153 ±11	0–435	0.97		55 ±5	0–328	1.22		16 ±0	9–26	0.29		20 ±0	10–27	0.20	
Male	141 ±7	0–435	0.94		74 ±4	0–328	0.95		17 ±0	9–28	0.28		21 ±0	10–28	0.19	
Female	119 ±1	0–581	0.87		70 ±1	0–479	0.82		19 ±0	5–29	0.27		21 ±0	8–29	0.18	
Mean	120 ±1	0–581	0.87		70 ±1	0–479	0.82		19 ±0	5–29	0.27		21 ±0	8–29	0.18	
Shortfin mako (<i>Isurus oxyrinchus</i>)																
38572F	121 ±2	0–441	0.67		86 ±1	0–328	0.57		16 ±0	6–25	0.25		18 ±0	9–25	0.18	
46583F	76 ±3	0–290	1.11		89 ±8	0–290	0.85		23 ±0	14–26	0.14		22 ±0	18–26	0.09	
Female	119 ±2	0–441	0.68		86 ±1	0–328	0.59		16 ±0	6–26	0.26		18 ±0	9–26	0.18	
Silky shark (<i>Carcharhinus falciiformis</i>)																
38573M	82 ±1	0–253	0.44		42 ±1	0–237	0.82		25 ±0	20–27	0.03		26 ±0	19–27	0.02	
38581F	65 ±2	0–161	0.53		62 ±2	0–167	0.63		26 ±0	23–26	0.02		25 ±0	15–26	0.05	
38599M	51 ±1	0–134	0.52		42 ±2	0–178	0.74		25 ±0	22–25	0.03		25 ±0	16–26	0.04	
38601M	92 ±1	0–237	0.38		42 ±1	0–151	0.75		24 ±0	19–27	0.04		25 ±0	22–27	0.02	
46564M	50 ±1	0–215	0.38		50 ±1	5–215	0.43		28 ±0	22–29	0.02		28 ±0	23–29	0.02	
46566M	35 ±1	0–86	0.49		45 ±1	0–97	0.48		28 ±0	25–29	0.02		28 ±0	22–29	0.03	
46585M	34 ±0	0–145	0.61		15 ±0	0–199	1.34		28 ±0	22–29	0.02		28 ±0	22–29	0.02	

continued

Appendix 2 (continued)

PSAT no. and sex	Day depth (m)			Night depth (m)			Day temperature (°C)			Night temperature (°C)			
	Mean ±SE	Min-max	CV	Mean ±SE	Min-max	CV	Lunar (R)	Mean ±SE	Min-max	CV	Mean ±SE	Min-max	CV
Silky shark (<i>Carcharhinus falciformis</i>) continued													
46588M	30 ±1	0-161	0.72	24 ±1	0-167	0.99	0.23	27 ±0	20-28	0.03	27 ±0	18-29	0.05
46590F	27 ±1	0-86	0.55	30 ±1	0-183	0.65		28 ±0	27-29	0.01	28 ±0	18-29	0.03
Male	58 ±0	0-253	0.65	34 ±0	0-237	0.90		27 ±0	19-29	0.07	27 ±0	16-29	0.06
Female	43 ±1	0-161	0.73	43 ±1	0-183	0.76		27 ±0	23-29	0.05	27 ±0	15-29	0.07
Mean	56 ±0	0-253	0.66	34 ±0	0-237	0.89		27 ±0	19-29	0.08	27 ±0	15-29	0.06
Oceanic whitetip shark (<i>Carcharhinus longimanus</i>)													
13092F	46 ±1	0-140	0.60	37 ±1	0-145	0.86	0.29	26 ±0	22-28	0.04	26 ±0	22-28	0.04
13113M	31 ±1	0-172	1.08	31 ±1	0-167	0.99	0.35**	27 ±0	17-28	0.05	27 ±0	22-28	0.03
38575M	28 ±1	0-264	1.20	30 ±1	0-178	1.03	0.20**	25 ±0	12-28	0.04	25 ±0	19-27	0.04
38576M	19 ±1	0-156	1.25	25 ±1	0-124	0.95	0.07	25 ±0	21-26	0.02	25 ±0	22-26	0.02
38582M	22 ±1	0-118	0.94	40 ±1	0-172	0.81	0.07	28 ±0	21-31	0.06	27 ±0	20-30	0.06
38598M	31 ±1	0-172	0.93	33 ±1	0-231	0.97	0.04	25 ±0	21-26	0.03	25 ±0	19-26	0.03
46568M	23 ±0	0-140	1.03	27 ±1	0-247	0.98	0.25*	26 ±0	20-28	0.03	26 ±0	13-29	0.04
46569M	24 ±1	0-108	0.82	33 ±1	0-151	0.77	0.45*	27 ±0	22-29	0.04	27 ±0	20-28	0.05
46570F	36 ±1	0-231	0.80	38 ±1	0-194	0.76	0.05	27 ±0	20-29	0.04	27 ±0	19-29	0.04
46581M	31 ±1	0-178	0.91	35 ±1	0-210	0.81	0.26**	27 ±0	21-30	0.04	27 ±0	21-30	0.04
46587M	27 ±1	0-242	1.19	35 ±1	0-280	1.02	0.12	27 ±0	19-29	0.04	27 ±0	18-29	0.05
46589F	32 ±1	0-167	0.77	30 ±1	0-317	0.89	0.07	26 ±0	20-29	0.04	26 ±0	18-28	0.04
Male	26 ±0	0-264	1.08	32 ±0	0-280	0.95		26 ±0	12-31	0.05	26 ±0	13-30	0.05
Female	36 ±1	0-231	0.77	35 ±1	0-317	0.82		27 ±0	20-29	0.04	26 ±0	18-29	0.04
Mean	28 ±0	0-264	1.02	32 ±0	0-317	0.93		26 ±0	12-31	0.05	26 ±0	13-30	0.05
Bigeye thresher (<i>Alopius superciliosus</i>)													
28476	297 ±4	22-506	0.29	105 ±2	5-409	0.67	0.009	11 ±0	6-21	0.28	19 ±0	7-27	0.22
29481	339 ±3	102-516	0.24	127 ±3	27-500	0.64	0.31*	12 ±0	6-24	0.35	20 ±0	6-27	0.23
46582	380 ±5	38-543	0.22	125 ±6	22-430	0.83	0.22	10 ±0	5-25	0.39	21 ±0	8-27	0.21
Mean	331 ±2	22-543	0.27	118 ±2	5-500	0.70		11 ±0	5-25	0.35	20 ±0	6-27	0.23

Appendix 3

Summary of Kruskal-Wallis nonparametric ANOVA tests with the data streams available in pop-up satellite archival tags (PSATs) for depth (day depth=DD, night depth=ND, combined depth=AD) and temperature data (day temperature=DT, night temperature=NT, combined temperature=AT) for each of the pelagic shark species. The Kruskal-Wallis test statistic (H_c) was adjusted for ties (Zar, 1996). Results for post-hoc pairwise Mann-Whitney (Bonferroni corrected P -values) (MWBC) tests are summarized for each of the pelagic shark species. Sample sizes and possible number of pairwise tests used in the comparisons are given for each species. Two sample Kolmogorov-Smirnov tests paralleled the results from pairwise MWBC tests (results not shown).

Species	Kruskal-Wallis	PSAT data stream/ comparison	Possible no. of pairwise Mann-Whitney tests (MWBC)	No. of significant MWBC tests	Percentage of significant MWBC tests
Blue shark (<i>Prionace glauca</i>) $n=14$	$H_c=1152$, $P=4.898-238$	AD	91	71	78.02
	$H_c=209$, $P=1.945-37$	DD	91	57	62.64
	$H_c=298.1$, $P=5.988-56$	ND	91	54	59.34
	$H_c=292.5$, $P=8.916-55$	AT	91	60	65.93
	$H_c=175.1$, $P=1.758-30$	DT	91	58	63.74
	$H_c=423.2$, $P=2.945-82$	NT	91	74	81.32
			Total 546	374	68.50
		DD vs. ND			
			1 (pooled) ¹	1	100.00
			1 (pooled: male) ¹	1	100.00
			1 (pooled: female) ¹	1	100.00
			14 (within)	12	85.71
			4 (between×pooled gender)	4	100.00
			182 (between)	150	82.42
		DT vs. NT			
			1 (pooled) ¹	1	100.00
			1 (pooled: male) ¹	1	100.00
			1 (pooled: female) ¹	1	100.00
			14 (within)	6	42.86
			4 (between×pooled gender)	3	75.00
			182 (between)	131	71.98
Bigeye thresher (<i>Alopias superciliosus</i>) $n=3$	$H_c=567.2$, $P=6.933-124$	AD	3	3	100.00
	$H_c=62.38$, $P=2.861-14$	DD	3	3	100.00
	$H_c=238.6$, $P=1.567-52$	ND	3	2	66.67
	$H_c=2.83$, $P=3.375-12$	AT	3	2	66.67
	$H_c=56.01$, $P=6.921-13$	DT	3	3	100.00
	$H_c=45.85$, $P=1.107-10$	NT	3	2	66.67
			Total 18	15	83.33
		DD vs. ND			
			1 (pooled) ¹	1	100.00
			3 (within)	3	100.00
			6 (between)	6	100.00
		DT vs. NT			
			1 (pooled) ¹	1	100.00
			3 (within)	3	100.00
			6 (between)	6	100.00
Oceanic whitetip (<i>Carcharhinus longimanus</i>) $n=12$	$H_c=1206$, $P=1.078-249$	AD	66	58	87.88
	$H_c=267.7$, $P=8.6-51$	DD	66	50	75.76
	$H_c=556.3$, $P=4.121-112$	ND	66	56	84.85
	$H_c=2101$, $P=0$	AT	66	56	84.85
	$H_c=463.4$, $P=2.726-92$	DT	66	54	81.82
	$H_c=978.2$, $P=1.71-202$	NT	66	59	89.39
			Total 396	333	84.09

continued

Appendix 3 (continued)

Species	Kruskal-Wallis	PSAT data stream/ comparison	Possible no. of pairwise Mann-Whitney tests (MWBC)	No. of significant MWBC tests	Percentage of significant MWBC tests
Oceanic whitetip <i>continued</i>		DD vs. ND	1 (pooled) ¹	1	100.00
			1 (pooled: male) ¹	1	100.00
			1 (pooled: female) ¹	1	100.00
			12 (within)	9	75.00
			4 (between × pooled gender)	3	75.00
			132 (between)	105	78.79
		DT vs. NT	1 (pooled) ¹	0	0
			1 (pooled: male) ¹	1	100.00
			1 (pooled: female) ¹	1	100.00
			12 (within)	9	75.00
			4 (between × pooled gender)	4	100.00
			132 (between)	121	91.67
Silky shark (<i>Carcharhinus</i> <i>falciformis</i>) <i>n</i> =9	$H_c=2265$, $P=0$ $H_c=643.7$, $P=1.347-133$ $H_c=259.5$, $P=2.092-51$ $H_c=581.4$, $P=2.938-120$ $H_c=907.2$, $P=2.154-189$ $H_c=1514$, $P=1.161-319$	AD	36	33	91.67
		DD	36	30	83.33
		ND	36	26	72.22
		AT	36	32	88.89
		DT	36	30	83.33
		NT	36	35	97.22
			Total 216	186	86.11
		DD vs. ND	1 (pooled) ¹	1	100.00
			1 (pooled: male) ¹	1	100.00
			1 (pooled: female) ¹	1	100.00
			9 (within)	5	55.56
			4 (between × pooled gender)	4	100.00
			72 (between)	57	79.17
		DT vs. NT	1 (pooled) ¹	1	100.00
			1 (pooled: male) ¹	1	100.00
			1 (pooled: female) ¹	0	0
			4 (between × pooled gender)	4	100.00
			9 (within)	8	88.89
			72 (between)	62	86.11
Shortfin mako (<i>Isurus oxyrinchus</i>) <i>n</i> =2		AD	11	1	100.00
		DD	11	1	100.00
		ND	11	1	100.00
		AT	11	0	0
		DT	11	0	0
		NT	11	0	0
			Total 6	3	50.00
		DD vs. ND	1 (pooled) ¹	1	100.00
			2 (within)	2	100.00
			2 (between)	2	100.00
		DT v. NT	1 (pooled) ¹	1	100.00
			2 (within)	1	50.00
			2 (between)	1	50.00

¹ For Mann-Whitney tests involving single comparison, Monte Carlo *P*-values are based on 10,000 random assignments.